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Plant Adaptations to Light Variability in the Boreal Mixed-Wood Forest

by

Kenneth James Greenway ©

A thesis submitted to the Faculty of Graduate Studies and Research in partial
fulfilment of the requirements for the degree of Doctor of Philosophy

Department of Renewable Resources

Edmonton, Alberta
Spring 1995

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled Plant Adaptations to Light Variability in the Boreal Mixed-Wood Forest submitted by Kenneth James Greenway in partial fulfilment of the requirements for the degree of Doctor of Philosophy.

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Abstract

In understory habitats, light quantity varies in time and space necessitating a range of adaptations that enable plants to utilise and withstand these variations. In a series of studies, the photosynthetic response to light was assesed is several species naturally growing in the understory of mixed-wood stands in west-central Alberta. Two trees of different successional positions (Picea glauca and Pinus contorta), a wide spread grass (Calamagrostis canadensis) and four shrubs differing in growth habit (Corylus cornuta, Lonicera involucrata, Rosa acicularis, and Rubus idaeus) were studied.

P. glauca is commonly found in the understory of hardwoods stands, yet also grows in the open under full light. P. contorta occasionally occurs in similar understory conditions, but usually grows in pure stands. After removal of the overstory (release) photosynthetic light response curves were developed to assess the short-term (days) photosynthetic response to the changed environment. P. glauca showed signs of damage to, and rapid recovery of, the photosynthetic system. P. contorta was mostly unaffected by release. Its photosystem appears adapted to high light. Long-term (years) effects of release in P. glauca included a large increase in photosynthetic area and photosynthetic rate. The season of release influenced shoot and crown morphology but the time of year of release had no immedieate detrimental effects.

The shrub and grass species studied are common in the understory of boreal mixed-wood stands, yet thrive in open conditions created by disturbances. The photosynthetic response to light in these species indicated a limited carbon assimilation ability at understory light levels. These low photosynthetic rates are sufficient to enable them to persist in the interval between disturbances, but would restrict growth and expansion in the understory.

With the exception of P. gluaca, the species studied have fire adapted reproduction mechanisms. The ability of the shrubs and C. canadensis to sustain an underground structure at understory light levels, and the serotinous cones in P. contorta, should ensure a presence on site immediately after a disturbance which will help to ensure rapid site re-vegetation. P. glauca has a range of adaptations to enable it to grow in low, high or changing light levels.

Acknowledgements

Although this thesis is authored by myself, it is the result of the collective work of numerous people. The constant encouragement and guidance of Vic and Ellen, my co-supervisors, were absolutely essential for the completion of this thesis. A special thanks to Elizabeth Marshall, who's contribution as a summer technician, though significant, was minuscule to the support and encouragement she gave me each day over these past several years. Michael Jones and Uldis Silins, and my other officemates, endured countless hours of technical questions, philosophical trifle, and endless complaining as I strove towards the completion of my thesis; without their support my task would have been considerably more onerous and much less rewarding. A note of thanks is also due to all the other graduate students for their helpful comments and criticisms as I toiled with my thesis. The assistance of summer technicians made this series of studies logistically possible. Their jobs were varied, tiresome and very often incredibly boring; to Brian Poole, Mark Conrad, Delinda Ryerson, Ancelm Mugasha, Tanya Lyons, Elizabeth Marshall, and Ken Stadt I extend a heartfelt "thank you".

Science is a discipline of sharing, and much of the equipment used in this thesis was borrowed from many people at the University of Alberta. I would like to thank: Dr. P. Crown, and Peter Gieb for use of, and help with, an image analysis system; Dr. S. Pawluk and Mike Abley for the use of, and help with, the thin sectioning image analysis system; Dr. J. Hoddinott for use of the spectroradiometer; Dr. P. Leavitt for some initial pigment trials with high performance liquid chromatography and to many others who provided technical advice and service for the equipment that was used. The faculty and staff of the then Department of Forest Science were also instrumental in aiding with day-to-day requirements of a graduate student, I thank them for their help. A note of thanks to the Forest Technology School, Hinton, and the Canadian Forestry

Service Field Camp, Hinton, for use of their facilities for laboratory space and lodging.

Research cannot be conducted without a considerable amount of dollars. The Natural Sciences and Engineering Research Council of Canada, through operating grants to my supervisors and four years of Post-Secondary Scholarships to myself, sustained this thesis. The financial assistance of Forestry Canada, five industrial partners, (Canadian Forest Products Ltd., Daishowa-Marubeni International Ltd., Procter and Gamble Cellulose Ltd., Weldwood Canada [Hinton Division] and Weyerhaeuser Canada Ltd. [Saskatchewan Division]), and the Canada-Alberta Partnership Agreement in Forestry is greatfully acknowledged. Supplemental bursaries to myself from Forestry Canada and the University of Alberta were also greatly appreciated.

Finally, I would like to express my gratitude to my parents, who have supported my education in many tangible and intangible ways, including the editing of a draft of this thesis.. Their constant love and support provided a solid foundation for these years of education. I thank them for the foresight to instill in me a hunger for knowledge and a desire to understand the world.

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Chapter One

General introduction

Plant Response to Resource Levels

For immobile organisms like plants, to use spatially heterogeneous resources (either above or below ground) they must produce leaves and/or roots in space so that the chance of acquiring these resources is maximised. Such non-random placement of plant "resource acquiring structures" has been compared to foraging behaviour (Hutchings and de Kroon 1994). Acclimation to spatially variable resources may require the production of new plant structures, whereas temporally variable resources may be fully utilised through changes in the physiology of existing structures. Thus through alterations in form or function, a plant may be able to utilise resources who's levels are spatially or temporally variable.

Alterations in plant morphology, anatomy, or physiology brought about by environmental conditions may be functionally classed as either plasticity or acclimation. Plasticity is the expression of variable phenotypes under sets of differing environmental conditions (Bradshaw 1965). Changes in a plant's phenotype as a result of *changing* environmental conditions has been termed acclimation, and is essentially a special case of plasticity (Strauss-Debenedetti and Bazzaz 1991). The distinction, though artificial, rests largely on whether a different phenotype is expressed through changes to an existing individual (acclimation) or whether the different phenotype is expressed in individuals growing in different environments. Historically, acclimation connotes an adaptive advantage from the changes in the phenotype, while phenotypic plasticity is not necessarily adaptive (Bradshaw 1965). The production of sun leaves in high fluence light and shade leaves in low fluence light is evidence of phenotypic plasticity. Alterations in leaf orientation and positioning on a shoot after a change in light fluence, however, is evidence of acclimation.

Changes in plant anatomy or morphology are generally expressed slowly as they involve the production of new tissue. If resource levels vary gradually, or are spatially heterogeneous, alterations in plant form may permit more effective acquisition or utilisation of the resource. If, however, resource levels change rapidly, then changes within existing tissue (physiological acclimation) may be the only means through which an individual can increase efficiency of resource capture or use. (Hutchings and de Kroon 1994).

The relative ability of an individual to maximise the acquisition or use of resources in heterogeneous environments will influence its ability to persist in these environments. In a similar fashion, the ability to alter structures and/or physiology in response to large fluctuations in the level of a resource may be crucial in preventing damage to, or death of, the plant. The extent to which acclimation can proceed in an individual depends on its inherent range of phenotypes (its phenotypic plasticity). The speed of the acclimation depends on the relative importance of the physiological versus morphological changes needed to produce a phenotype suited to the new conditions. Thus in environments characterised by variability in resource levels, morphological and physiological adjustments to plant form and function are crucial for survival.

Plant Response to Variability in Light

Light is fundamental to plant growth, yet its fluence rate (photon flux density) may be highly variable both spatially and temporally; this is particularly true in environments characterised by multi-layered canopies. The range of light environments in which plants of many forms are found, from the deep shade of the understory to the full light of open areas, is evidence of their ability to efficiently capture and utilise the available light.

Numerous studies, from subcellular to whole plant level, have investigated the nature of the change in physiology when plants are grown under, and/or transferred to, different intensity light environments (for reviews see Boardman 1977; Björkman 1981; Grime 1981; Evans et al. 1988). Much research on the very short-term variability in light (sunflecks) and the impact that this highly variable light has on understory vegetation is also available (for reviews see Chazdon 1988; Pearcy 1990; Chazdon and Pearcy 1991). Stomatal responses to dynamic light environments can modify the trade-off between carbon gain and water loss (Knapp and Smith 1990); this has been found in plants of various growth forms from many environments (Knapp and Smith 1991; Knapp 1992, 1993; Roden and Pearcy 1993a; Tinoco-Ojanguren and Pearcy 1993a,b). Changes to plant morphology in response to light, either at the whole plant or shoot level, have been studied less extensively (see review by Givnish 1988).

Forest Light Environments

In forested environments, understory light varies in both quality and quantity; its fluence rate may vary over time scales that range from seconds to decades (Ross et al. 1986; Cannell and Grace 1993; Brown and Parker 1994). Changes to the overstory canopy will alter the spatial and temporal distribution of light. Gradual changes in understory light fluence rate may be the result of changes in canopy characteristics such as trees' age or changes in the composition of species that dominate the canopy. Rapid alterations in understory light may be brought about by the formation of canopy gaps produced by tree mortality, or through disturbances (i.e. insect outbreaks or severe fires) removing large portions of the overstory.

In the boreal forest, large scale fire disturbances have created a mosaic of large even-aged stands (Heinselman 1981; Payette 1992). In western Canada, a short fire return interval has ensured that most of the stands are relatively young and predominantly even-aged. At the high latitudes where boreal forest are found (low solar angles for much of the year), canopy gaps must be very large to allow high fluence light to penetrate to the forest floor. Much of the increased light is spread into areas immediately adjacent to the gap (Canham et al. 1990). Individual tree-fall gaps and the multi-layer diverse canopies are common in tropical and many broad-leaved temperate forests and the ecology of such canopy dynamics have been extensively studied (Pickett and White 1985, Kolsa and White 1991). For the most part similar canopy gaps do not play a significant role in ecology of boreal forests understories, with the exception of areas that have escaped fire disturbance for prolonged periods (Kuuluvainen 1994). Tropical and temperate forest overstory-understory dynamics and the associated light environments are very dissimilar from those of the boreal forest, therefore the plant strategies in the understory are also likely to differ. Studies of light characteristics of the boreal forest (Ross et al. 1986; Lieffers and Stadt 1994; Constabel 1995) have documented mean light levels beneath canopies of different ages and structures, and generally show lower light levels below conifer dominated canopies. Aspen (Populus tremuloides Michx.) dominated stands have increased understory light fluence rate as stands age, so mature aspen stands can have high (30% full sun) ambient understory light levels (Lieffers and Stadt 1994). The majority of light reaching the lower portion of aspen canopies is in the form of short duration sunflecks (Roden and Pearcy 1993b).

The response of temperate coniferous tree growth (height and diameter) to differing light environments is well documented, but studies of changes in tree physiology or morphology that mediate this growth response are few. The effects of a changed light environment on the growth of economically valuable timber species are numerous (Ferguson and Adams 1980; Helms and Standiford 1985; Oliver 1986; McCaughey and Ferguson 1988; Yang 1989; Oliver and Dolph 1992; Navratil et al. 1994). The effect of differing light levels on shoot morphology, needle anatomy (Tucker and Emmingham 1977; Drew and Ferrell 1977; Leverenz and Jarvis 1980a,b; Zutter et al. 1986; Tucker et al. 1987) and crown architecture (Kohyama 1980; Greis and Kellomäki 1981) have been documented for several conifers. Very few studies on boreal forest tree species' response to light exist, except that of Lieffers et al. (1993) on released white spruce and Roden and Pearcy (1993a) on aspen. Ecophysiological research on boreal forest understory species is non-existent.

Much of the research dealing with the physiology of photosynthetic adaptations to variability in light supply, and the ecological significance of those plant adaptations, has been done with well studied crop species (tomato, sunflower etc.) or in the context of tropical forestry systems. While the underlying biochemical adaptations to high or low fluence light are likely shared among diverse species, the ecological role of such adaptations is not necessarily transferable to boreal forests. This is particularly true since the nature of canopy changes in tropical and temperate deciduous forest are dissimilar from those of the western Canadian boreal forest.

The Boreal Mixed-Wood Forest Species Dynamics

In much of the western Canadian mixed-wood boreal forest, white spruce (Picea glauca (Moench) Voss) and trembling aspen are common co-occurring trees. In many cases the rapid early growth of aspen will enable it to form a canopy over the spruce, however, since the spruce is longer lived, in the absence of disturbance it will become the dominant canopy tree (Lees 1966). Over succession the light environment in a boreal forest site changes: from the open, full-sun conditions immediately after fire, to reduce light levels as hardwood canopy closure occurs, and finally to the heavy shade of conifer stands (Ross et al. 1986; Lieffers and Stadt 1994). An individual spruce tree will have considerable variation in ambient light as it grows into an aspen canopy. Similarly, understory shrub and grass species, must survive these variations in the available light if they are to persist.

In the current work a series of experimental and descriptive studies on the nature of plant adaptations to these light conditions is described. The studies were designed to investigate, under natural field conditions, the photosynthetic system's response to light. Plant adaptations to variability in light may occur in many forms (biochemical, anatomical, or morphological) and at many levels of plant organisation (chloroplast, leaf, or crown). Photosynthesis is a function of all these factors and, as such, can act as an integrated measure of plant adaptation. Survival in the understory is inextricably linked to maintaining, as an absolute minimum, a photosynthetic system capable of supplying energy to meet respiratory demands. Therefore, a failure of the photosynthetic apparatus to acclimate to the prevailing light environment will result in the plant's inability to survive. An understanding of the nature of the photosystem in naturally occurring understory plants, as well as its potential to acclimate to changes in light intensity, is a good first step in understanding how plants are adapted to grow in these environments.

Photosynthetic light response curves were used to provide insight into more than the instantaneous photosynthetic potential. By understanding the relationship between carbon assimilation and light level, inferences about the potential carbon gain under different light regimes are made possible. Furthermore the use of gas exchange techniques enables the investigation into the stomatal limitations to photosynthesis and can yield some insights into the leaf-level mechanism of the photosynthetic process.

Overview of Studies

In mixed-wood stands of the boreal forest, many plant species exist in the understory but also thrive in open conditions. White spruce individuals can adjust to a change from understory to open conditions, but the nature of the response of the photosystem to this change was unknown. The short term (11 day) changes in the photosynthetic response to light fluence rate in white spruce was monitored after removal of overstory vegetation (release) (Chapter 2). The mid-to-late successional spruce was contrasted to the early succession lodgepole pine (Pinus contorta Dougl.) to assess how their photosystems would respond to release. These two commercially important timber species differ in that while light levels to which the spruce is subject to during its life span may be highly variable, in the pine the light is consistently at levels near that of full-sun. In the second study (Chapter 3) the longer-term (two years) alterations in white spruce crown and shoot morphology, and shoot photosynthesis were studied. Furthermore, the role of the season in which the overtopping vegetation was removed in altering morphological changes was investigated. The photosynthetic response to light in the common boreal forest grass Calamagrostis canadensis Michx (Beauv.) was investigated by developing light response curves in shade-grown and sun-grown plants (Chapter 4). Additionally the stomatal response to fluctuating light was assessed to establish the importance of short-term temporally variable on the potential for carbon assimilation in this grass. This grass grows in reduced amounts in the understory of boreal mixed-wood and broad-leaved stands but also dominates many open sites. Similarly, the nature of the photosynthetic response to light levels was studied in four boreal forest shrubs using gas exchange techniques (Chapter 5). Wild rose (Rosa acicularis Lindl.), wild red raspberry (Rubus idaeus L.), honeysuckle (Lonicera involucrata (Richards.) Banks) and hazelnut (Corylus cornuta Marsh.) represent three families with different above-ground forms, yet all are commonly found in the understory as well as open environments in the western Canadian boreal forest.

The understory and open environments in which all these species may be commonly found, differ greatly. This work provides information as to the nature of the photosystems of these species that enable them to persist in the understory and the nature of the response in white spruce and lodgepole pine individuals to an abrupt change from an understory to an open environment.

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Chapter Two

Effects of overstory vegetation removal on the photosynthesis of two boreal forest conifers: Inferences about plasticity

Introduction

Plasticity allows for variable phenotypes in different environments, thereby potentially conferring some adaptive advantage to the individual through better capture and use of essential resources. Phenotypic plasticity may be exhibited by changes in existing organs (acclimation) or through the expression of different phenotypes in different environments (plasticity) (sensu Strauss-Debenedetti and Bazzaz 1991). It has been suggested that early successional species have greater physiological flexibility than late successional species (Bazzaz 1979) and that this may be due to the amount of environmental variation characteristic of the species' typical habitat (Bazzaz and Carlson 1982). Photosynthetic studies have provided evidence that both support (Bazzaz and Carlson 1982; Strauss-Debenedetti and Bazzaz 1991) and contend (Oberbauer and Strain 1984; Walters and Field 1987; Turnbull 1991; Turnbull et al. 1993) this theory. This would suggest that successional status alone is a poor indicator of photosynthetic plasticity, and that a more comprehensive understanding of the species' autecology may be necessary to make predictions about its photosynthetic plasticity. The extent and pattern of variability in relevant environmental variables during an individual's life-span, may be a better indicator of a trait's plasticity in a given species than merely its successional position.

In the boreal forest of western North America, white spruce (Picea glauca (Moench) Voss) commonly forms an understory to aspen (Populus tremuloides Michx.). In the absence of disturbance, white spruce will form the dominant canopy tree in later successional stages when the aspen die (Lees 1966). In addition to this variability in light over the succession time period, the light levels fluctuate seasonally under an aspen canopy due to its deciduous habit (Constabel 1995) and the nature of the canopy (Roden and Pearcy 1993). In contrast, lodgepole pine (Pinus contorta var. latifolia Engelm.) is a fire-regenerated, shade intolerant species typically existing in pure stands (Lotan and Critchfield 1990). Both at the seasonal and successional time frames, lodgepole pine will usually experience a relatively constant, high fluence, light environment. It may, however, form an understory to aspen in montane areas and in managed forests where cultural techniques result in both species co-occurring. As both species are shade intolerant, high densities of either will generally reduce the growth of the other. Vegetative regeneration in aspen and its rapid growth rates may enable it to overtop lodgepole pine seedlings, resulting in understory lodgepole pine.

The manual removal of competitive species (brushing or release) during the conifer juvenile phase, is a common silvicultural practice aimed at increasing conifer growth. Lieffers et al. (1993) showed that two weeks after release, sapling white spruce had a depression in light saturated photosynthetic rates. Within 4 weeks, however, released trees had recovered to control tree levels. The nature of the initial depression in photosynthesis was not identified.

In this study, in situ photosynthetic light response in the immediate short term was measured immediately after the removal of an overtopping hardwood canopy. Photosynthetic response to light in intact shoots of white spruce and lodgepole pine were measured using gas exchange techniques. By investigating photosynthetic responses using gas exchange techniques, we were able to address the underlying mechanisms of any limitations to the photosynthetic process. Few studies have attempted to quantify field photosynthetic light response, none have done so with either white spruce or lodgepole pine. Studies of such photosynthetic variables in temperate spruce are limited to the work on Sitka spruce (Picea sitchensis (Bong.) Carr.) (Ludlow and Jarvis 1971; Leverenz and Jarvis 1980), and the work of Leverenz on the nature of the photosynthetic light response curves in a number of Picea species, including white spruce, and Pinus sylvestris L. (Leverenz 1987, 1988).

The objective of this study was to investigate the short term photosynthetic response in sapling white spruce and lodgepole pine to the removal of the aspen overstory. Based on the typical variation in light environment these species experience over their life-span, it was hypothesised that white spruce would show greater photosynthetic adjustment to the new conditions created by release than would lodgepole pine.

Materials and Methods

The study site was on a bench of the Athabasca river, 13 km northeast of Hinton, Alberta (53°32' N, 117°27' W). A one hectare area of sapling white spruce growing under 3-4 m aspen and an adjacent (50m) 2 ha area of aspen and lodgepole pine were chosen. On one half of the spruce area all aspen trees were cut. Six spruce saplings were randomly assigned as study trees in the brushed area; an additional six were chosen as controls in the unbrushed area. The aspen canopy over the lodgepole pine was patchy, so individual trees were randomly assigned to be either released or serve as controls. All vegetation within a 2 m radius of a sample pine was removed so that no significant shade fell on any released tree between 0900 and 1700 hrs for the duration of the experiment. Sampled tree heights ranged from 1 to 1.5 m for spruce, and 1.5 to 2 m for lodgepole pine. Brushing was applied only after full needle expansion was complete, and occurred on July 29, 1991 for spruce and August 15, 1991 for pine. For both species, the release treatment was followed by at least 7 consecutive days of sunny, hot weather.

Including set-up and equilibration time at each light level, a maximum of 12 trees/day could be measured. Thus, to ensure an acceptable sample size in each species, they were studied in two separate experiments, the first with white spruce and the second with lodgepole pine. Although the two species cannot be compared statistically, the two week time span between the experiments should not have altered their responses significantly thus allowing qualitative comparison between them. Gas exchange was measured on current tissue (1991), on an intact whole shoot in spruce and 3-4 fascicles in pine. The pine needles were spread flat in the leaf chamber to avoid self-shading. Photosynthetic response to light was measured on all 12 trees the day before release and on 1, 2, 3, 4 ,5, 11, and 30 days after brushing, except in lodgepole pine, where measurements were not taken on day 30 due to occurrence of frost 23 days after treatment application.

Photosynthesis was measured between 0930 and 1700 hrs to ensure measurements did not contain errors from dew in the morning, or continue too late in the afternoon. South-facing branches on the third whorl from the top were selected in spruce and from the 3rd or 4th whorl in pine. Control and released trees were paired in time during measurements to account for diurnal changes in photosynthesis. Photosynthetic light response (based on incident light) was measured at four light levels (approximately 150, 400, 750, 900 μmol m^{-2} s^{-1}) with one dark respiration measurement taken after a 5 minute dark acclimation period. All gas exchange measurements were made using an open system, LCA-3 portable infra-red gas analyser (Analytical Development Corp., Hoddenson, UK) and conifer cuvette (PLC (C)). In-going relative humidity was maintained between 30 and 40%. Photosynthesis reached a steady state level within 5-7 minutes at each light level in both species.

A photon flux density controller (PFDC) was constructed to provide variable light levels. The light source was a 50 watt quartz halogen flood lamp (Osram coolspot #41870) powered by a 12 volt regulated gel-cell battery pack.

The light was passed through a 50 mm camera lens and light fluence rate was controlled by manipulating the lens diaphragm. A blue filter (Roscolux Cool Blue #66, Rosco, Port Chester, NY) was used to reduce red light (580-670 nm) transmission by 60%. A diffuser (Rosco Cinegel - half density soft frost #3004, Rosco, Port Chester, NY) was used to diffuse light and dark areas produced by the bulb's multi-reflector design. The PFDC was mounted on the Plexiglas infra-red shield of the cuvette. The PFDC and the cuvette chamber were surrounded by a cloth bag to exclude ambient light. Light calibration was done with a Li-Cor quantum sensor (LI-190SB, Li-Cor. Ltd., Lincoln, NB) placed inside the cuvette chamber. Some unevenness in light distribution within the leaf chamber was accounted for by calculating a weighted mean light level for each shoot (or needles in pine) based on the shoot length (or mean needle length).

Estimates of spruce needle-air temperature differences due to incident light, were established by inserting fine copper-constantan thermocouples (Omega Engineering, Stamford, CN) into needles on the sides of representative spruce shoots. For the five light levels used, needle-air temperature differences averaged -0.34, 0.0, 0.71, 1.15, and 1.37 °C (n=5); these values were used in subsequent photosynthesis calculations. Needle-air temperature differences for the pine were -0.34, 0.0, 1.40, 2.00, and 2.48 °C for the five light levels used.

Net assimilation rate (NA; μmol CO_2 m^{-2} s^{-1}), stomatal conductance to CO_2 (g_c; mmol m^{-2} s^{-1}) and transpiration rate (E; mmol H_2O m^{-2} s^{-1}) were calculated according to the equations of Caemmerer and Farquhar (1981); residual conductance (g_r; mmol CO_2 m^{-2} s^{-1}) was calculated as NA / internal CO_2 concentration (Jones 1985). All photosynthesis variables were expressed on a total leaf area basis for comparison between species. Photosynthetic variables expressed on a shoot silhouette area basis showed identical trends in spruce(data not shown). Total leaf area (TLA) was estimated from projected leaf area (PLA) measured with the LI-3100 leaf area meter (LI-Cor., Lincoln, NB) using a regression equation derived for each species. For random samples (40 spruce and 20 pine of 5 needles per tree) TLA was calculated from the mean perimeter of three cross-sections of each needle taken at the mid, upper, and lower third, and multiplied by the needle length. Sections were hand-digitised and perimeters measured by an image analysis system (Karl Zeiss Ltd., Germany). TLA was summed for the five needles and regressed against their projected area. Regression equations were - Spruce: TLA = 0.344 + 2.83(PLA.), $r^2 = 0.95$ and Pine: TLA = 0.685 + 3.058(PLA), $r^2 = 0.89$.

Light response curves were developed by fitting the data to the monomolecular function described by Causton and Dale (1990) using a non-linear iterative curve fitting routine. The model,

$$NA = a * \left[1 - e^{(b - c * PPFD)}\right]$$

describes an increase in net assimilation rate (NA) to an asymptotic maximum at *a* with increasing photosynthetic photon flux density (PPFD). The additional parameters *b*, and *c* control the rate and shape of the approach to the maximum rate. Derived variables from the model light response curves included respiration rate (μmol CO_2 m^{-2} s^{-1}) calculated as $a(1-e^{b})$; light compensation point (μmol photons m^{-2} s^{-1}), the value of PPFD where NA is zero and is equivalent to b/c; photochemical efficiency (μmol CO_2 μmol^{-1} photon), the slope of the function at a PPFD of zero and is calculated as ace^{b}; and maximum light saturated photosynthetic rate (A_{max} ; μmol CO_2 m^{-2} s^{-1}) equivalent to the asymptote *a* (Causton and Dale 1990). In order to ensure a reasonable fit of the model, all data points were used in the non-linear regressions. The use of data below the area of the light compensation point will over estimate quantum yield (Sharp et al. 1984). The efficiency of light use has been termed photochemical efficiency in this work to distinguish it from the true quantum yield.

Curves were fit to control and released data sets (as groups) and to individual trees for estimates of variables derived from the light response curves. Differences between light response curves of control and released trees on any one day were examined by testing for coincident regression (Potvin et al. 1990). Measured and derived variable means were compared between released and control on any one day using one-way analysis of variance.

Results

Spruce

There were no differences in light-saturated photosynthetic assimilation rate in released and control trees prior to and on the day after release. However, from day 2 through day 5 and on day 11, light saturated net assimilation was significantly lower (by as much as 30%) in released trees (Fig. 2-1A and Table 2-1). Thirty days after release, however, this difference was no longer apparent. A similar pattern was shown in residual conductance (Fig. 2-1B), while stomatal conductance did not differ significantly between control and released trees except on the second day after brushing (Fig. 2-1C and Table 2-1). Transpiration rates were similar in control and released trees for the duration of the experiment and ranged from 0.25 to 0.80 mmol H_2O m^{-2} s^{-1}.

Photosynthetic light response curves (Fig. 2-2) were similar for control and released trees prior to and one day after release. For days 2 through 11 after brushing there was a significant change in the photosynthetic light response of the released trees relative to controls (Table 2-2). Recovery of the photosynthetic rates to control tree levels was seen in released trees on day 30. Respiration rates ranged from 0.70 to 1.32 μmol CO_2 m^{-2} s^{-1} in control trees and 0.79 to 1.46 μmol CO_2 m^{-2} s^{-1} in released trees, but did not differ significantly between groups. The photochemical efficiency of released trees dropped over the course of the experiment, so that following day 5 it was significantly lower than in control trees (Table 2-3). Photosynthetic light compensation points were higher in released trees than in the controls. Maximal light-saturated photosynthesis rates followed the same trend as measured photosynthetic rates, and showed significantly lower A_{max} in released trees on days 2 through 11 (Table 2-3).

Pine

The lodgepole pine photosynthetic response to release more variable than in white spruce. Net assimilation and residual conductance were significantly lower in released trees on day 5 only (Fig. 2-1D,E and Table 2-1). As in the white spruce, transpiration rates in released trees did not differ from control tree levels and ranged from 0.30 to 0.85 mmol H_2O m^{-2} s^{-1}. Stomatal conductance also did not differ between groups for the duration of the experiment (Fig. 2-1F and Table 2-1). Respiration rates ranged from 0.60 to 0.93 and 0.61 to 1.2 mmol CO_2 m^{-2} s^{-1} in control and released trees respectively, but were not significantly different between the two groups.

Control or released lodgepole pine light response curves (Fig. 2-3) did not differ significantly after release except on days 2 and 5 (Table 2-4). Considerable variability in response between individual trees (in both groups) was evident after release. Photochemical efficiency did not differ between control and released trees at any time during the experiment (Table 2.4). Light compensation points and A_{max} were generally similar between groups with the exception of day 5. On this day significantly lower A_{max} in released trees coupled with an unchanged respiration rate, resulted in a higher light compensation point (Table 2-4).

Discussion

The reduction in light-saturated NA after brushing in white spruce indicated that white spruce photosynthetic systems had been depressed when exposed to full sun-light. The lack of a consistent reduction in lodgepole pine photosynthetic rates indicated a photosystem unaffected by the change in light brought about by the release treatment. It would seem that these understory spruce were shade phenotypes adapted to low light conditions, while the understory lodgepole pine trees were not. Several lines of evidence support this assertion. The significant reduction in measured light-saturated NA (and modelled A_{max}) in released white spruce trees lasted for 11 days after treatment, and indicated a substantial alteration in the photosynthetic process. The lack of significant changes in transpiration and stomatal conductance suggested that plant water status effects stomatal control of photosynthesis were not likely a contributing factor. The reduction in photochemical efficiency and residual conductance indicated that the depression in measured photosynthesis may have been biochemical in nature. Damage to pigments following transition of low fluence light grown plants into high fluence light is well documented for numerous species (Powles 1984 and references within) and may account for the noted reduction in photochemical efficiency found in this study. Although the precise nature of the damage to the spruce photosystem is not known, the significantly altered photosynthetic light response curves are clear evidence of a changed photosynthetic response to light.

The findings for white spruce demonstrated considerable photosynthetic plasticity. The photosystem was depressed after exposure to high fluence light and showed rapid acclimation to the new condition created by the release treatment. Long term adjustment in released white spruce enabled them to surpass control tree photosynthetic rates (Lieffers et al. 1993, Chapter 3) and increased diameter growth after release (3-5 yrs) has been extensively documented (Berry 1982; Yang

1989; Navratil et al. 1994). These release studies show a remarkable ability in white spruce to acclimate to high fluence light environment. In contrast, the lack of any consistent reduction in any measured variable in lodgepole pine after release suggested this species did not form a shade phenotype in the understory. In addition, the understory pine trees had the narrow boles and few branches and needles, these are typical morphologic characteristics of shade avoiders (Smith 1982). Even under high aspen competition levels, young lodgepole pine trees have significantly reduced diameter growth but little reduction in height growth (Navratil and MacIsaac 1993) which indicates a shade avoidance strategy (Grime 1981).

Several ecological factors may explain the greater physiological plasticity in the mid-successional white spruce relative to the early successional lodgepole pine. Light levels in aspen-dominated stands are variable, both temporally and spatially. Periods of leaflessness in the overstory and characteristics of aspen crowns result in considerable variability in understory light (Ross et al. 1986; Roden and Pearcy 1993; Constabel 1995). Mid-summer transmission to a 1.3 metre height in aspen stands of similar age can range from 10-33% of full sun (Constable 1995). These levels are clearly sufficient to enable understory spruce to photosynthesise at near maximum rates as found in this study. White spruce can be found growing in pure stands in full light and when found in the understory of aspen stands will, over succession, come to dominate the canopy. White spruce can respond positively to release from overstory vegetation even after 40-50 years of suppression (Lees 1966; Berry 1982). The evidence from this study indicated that this positive response to release is based in part upon the ability of white spruce to rapidly acclimate light levels dramatically different from those under which it is growing.

Studies of other conifers released from conifer overstories report growth reduction and needle loss in the released trees (Tucker and Emmingham 1977;

Tucker et al. 1987). Such responses may be related to the very low light levels in the understory of such stands. The light level under aspen canopies, however, are relatively high compared to spruce-fir dominated stands (Ross et al. 1986; Lieffers and Stadt 1994). The current evidence of a plastic response to altered light environment coupled with the broad range of light environments in which white spruce can successfully grow (Nienstaedt and Zasada 1990) suggests a generalist's approach to light utilisation.

Lodgepole pine, in contrast, does not grow well under a heavy overstory and is a shade intolerant species (Lotan and Critchfield 1990). It is a fire regenerated species and its rapid initial growth in post-fire open areas may help to ensure that it stays above much of the competing vegetation. The lack of evidence of a depression in its photosynthetic rate after release, may be attributed to a specialised photosynthetic system that permits existence under some level of shade, but that is adapted to full sunlight conditions.

In studying niche breadths, Parrish and Bazzaz (1982) found similar broad responses to light gradients in early and late successional temperate trees, although on moisture and nutrient gradients, early successional species showed broader responses than late successional species. The results from this study on white spruce and lodgepole pine photosynthesis are consistent with their findings. Photosynthetic plasticity may be more accurately predicted from a knowledge of the species' autecology rather than from their successional status alone. Long-term temporal heterogeneity has been found to be associated with physiological flexibility in late successional tropical tree species (Pearcy 1987) and the same is true with regards to the photosynthetic system plasticity in these two boreal forest conifers.

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Table 2-1. P values for ANOVA test of significant difference in measured light saturated photosynthesis variables between control and released trees for lodgepole pine and white spruce prior to and following overstory vegetation removal.

	White Spruce			Lodgepole Pine		
Days since release	Assimilation Rate ($\mu mol\ m^{-2}\ s^{-1}$)	Residual Conductance ($mmol\ m^{-2}\ s^{-1}$)	Stomatal Conductance ($mmol\ m^{-2}\ s^{-1}$)	Assimilation Rate ($\mu mol\ m^{-2}\ s^{-1}$)	Residual Conductance ($mmol\ m^{-2}\ s^{-1}$)	Stomatal Conductance ($mmol\ m^{-2}\ s^{-1}$)
Pre[1]	0.324	0.343	0.856	0.622	0.622	0.604
1	0.672	0.631	0.690	0.864	0.769	0.688
2	0.041	0.035	0.037	0.080	0.066	0.213
3	0.028	0.031	0.325	0.277	0.182	0.224
4	0.018	0.014	0.193	0.477	0.443	0.732
5	0.067	0.058	0.860	0.007	0.007	0.376
11	0.036	0.028	0.459	0.337	0.314	0.652
30	0.438	0.412	0.267	--[2]	--	--

[1] Pre-release measures

[2] Data not collected

Table 2-2. Test for coincidence (P) of best fit non-linear regression lines of pooled control and released tree (n = 6 trees per treatment) net assimilation rate versus incident photosynthetic photon flux density.

Days Since Release	White Spruce	Lodgepole Pine
Pre[1]	0.168[2]	0.279
1	0.325	0.839
2	<0.001	0.013
3	<0.001	0.210
4	<0.001	0.332
5	<0.001	<0.001
11	<0.001	0.118
30	0.051	---[3]

[1] Pre-release measures

[2] P value for $F_{3,52}$

[3] Data not collected

Table 2-3. Means (±SE n = 6) of variables derived from modelled non-linear light response curves and P values for ANOVA test, on each day, for significant differences between control and released white spruce saplings.

Days since release	Photochemical Efficiency (μmol photon μmol^{-1} CO$_2$)			Light Compensation Point (μmol photon m^{-2} s^{-1})[1]			A_{max} (μmol CO$_2$ m^{-2} s^{-1})[1]		
	Control	Released	P[2]	Control	Released	P	Control	Released	P
Pre[3]	0.024	0.022	0.520	36.68	53.13	0.06	2.55	2.31	0.535
	(0.002)	(0.003)		(4.85)	(7.63)		(0.28)	(0.24)	
1	0.022	0.018	0.107	36.44	49.27	0.02	2.71	2.69	0.971
	(0.001)	(0.002)		(2.39)	(4.08)		0.18	(0.18)	
2	0.020	0.015	0.206	60.10	90.07	0.11	1.87	1.15	0.049
	(0.003)	(0.003)		(10.72)	(13.04)		(0.167)	0.278	
3	0.021	0.014	0.046	44.22	81.75	0.06	2.17	1.53	0.022
	(0.003)	(0.002)		(6.93)	(16.32)		(0.170)	(0.166)	
4	0.021	0.017	0.244	69.32	101.50	0.25	1.98	1.12	0.031
	(0.003)	(0.002)		(15.57)	(21.65)		(0.32)	(0.11)	
5	0.021	0.013	0.030	100.53	187.94	0.04	1.23	0.34	0.018
	(0.003)	(0.001)		(26.94)	(34.02)		(0.28)	(0.18)	
11	0.033	0.020	0.004	51.90	123.53	0.02	2.01	1.26	0.038
	(0.003)	(0.003)		(6.26)	(24.58)		(0.20)	(0.24)	
30	0.022	0.017	0.002	31.39	60.24	0.01	2.71	2.49	0.559
	(0.001)	(0.001)		(4.88)	(7.97)		(0.31)	(0.19)	

[1] Expressed on a total leaf area basis

[2] Probability value of $F_{1,10}$

[3] Pre-release measures

Table 2-4. Means (±SE n = 6) of variables derived from modelled non-linear light response curves and P values for ANOVA test, on each day, of significant difference between control and released lodgepole pine saplings.

Days since release	Photochemical Efficiency (μmol photon μmol^{-1} CO_2)			Light Compensation Point (μmol photon m^{-2} s^{-1})[1]			A_{max} (μmol CO_2 m^{-2} s^{-1})[1]		
	Control	Released	P[2]	Control	Released	P	Control	Released	P
Pre[3]	0.028	0.014	0.214	42.99	48.81	0.60	1.94	1.73	0.505
	(0.010)	(0.002)		(6.86)	(8.49)		(0.26)	(0.15)	
1	0.015	0.016	0.586	72.77	64.56	0.74	2.12	2.03	0.872
	(0.001)	(0.003)		(17.59)	(15.10)		(0.30)	(0.472)	
2	0.017	0.013	0.261	68.04	92.56	0.17	2.17	1.56	0.145
	(0.002)	(0.002)		(8.78)	(13.99)		(0.32)	(0.228)	
3	0.025	0.024	0.765	56.95	69.84	0.65	1.77	1.36	0.218
	(0.010)	(0.003)		(9.66)	(16.42)		(0.18)	(0.25)	
4	0.020	0.016	0.203	52.16	59.06	0.28	2.23	2.02	0.536
	(0.002)	(0.001)		(7.26)	(9.65)		(0.26)	(0.213)	
5	0.022	0.015	0.108	35.77	59.55	0.02	2.58	1.81	0.001
	(0.003)	(0.002)		(4.00)	(7.21)		(0.08)	(0.151)	
11	0.014	0.015	0.709	47.22	61.61	0.36	2.29	2.12	0.493
	(0.001)	(0.003)		(7.02)	(7.32)		(0.18)	(0.15)	

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[1] Expressed on a total leaf area basis

[2] Probability value of $F_{1,10}$

[3] Pre-release measures

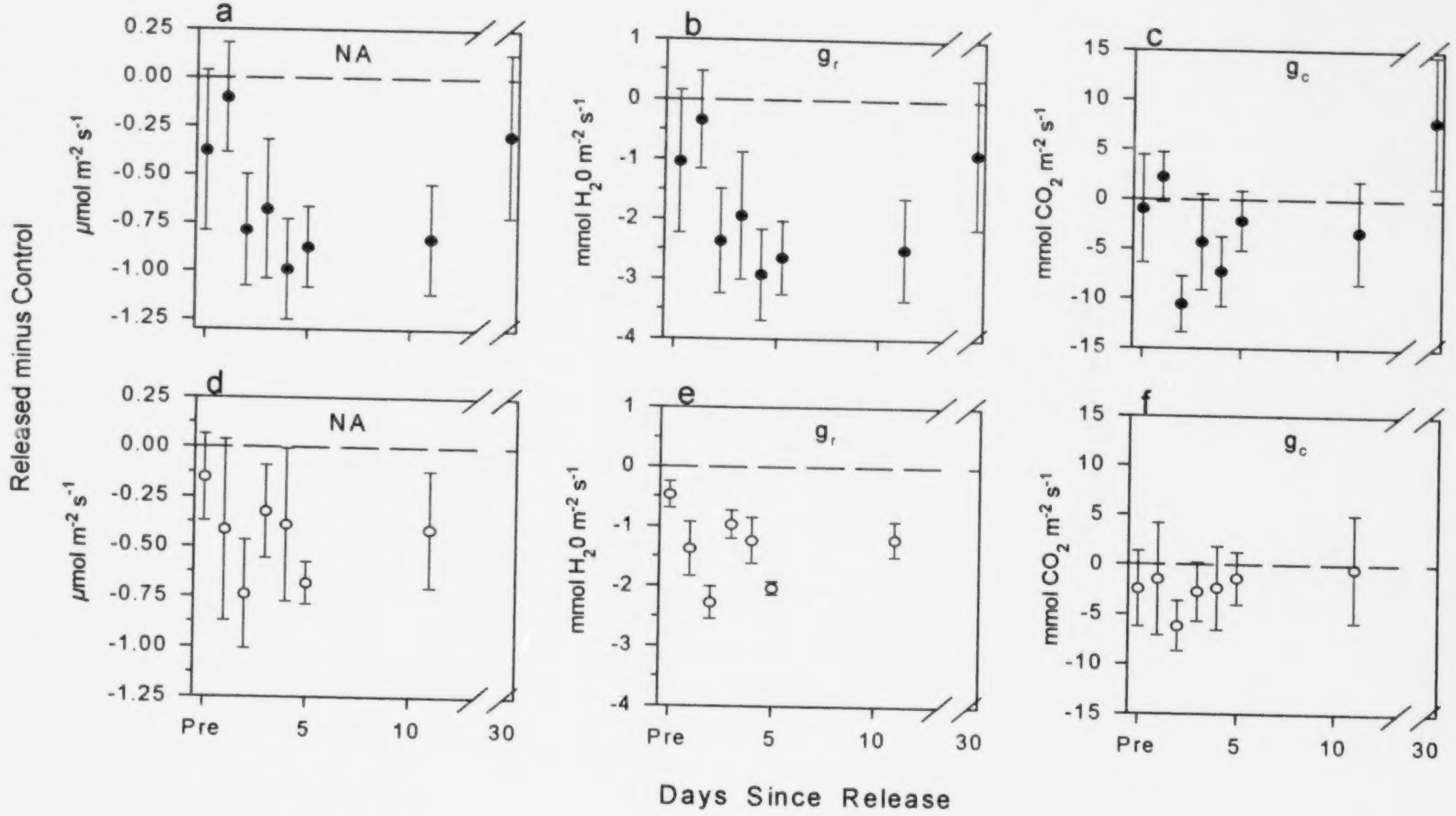

Figure 2-1. Means (± 1 SE) of differences between paired brushed and control trees for gas exchange variables measured at maximum photon flux density for the day prior to and several days after overstory vegetation removal. White spruce: a-c lodgepole pine: d-f. NA, net assimilation; g_r, residual conductance; g_c, stomatal conductance.

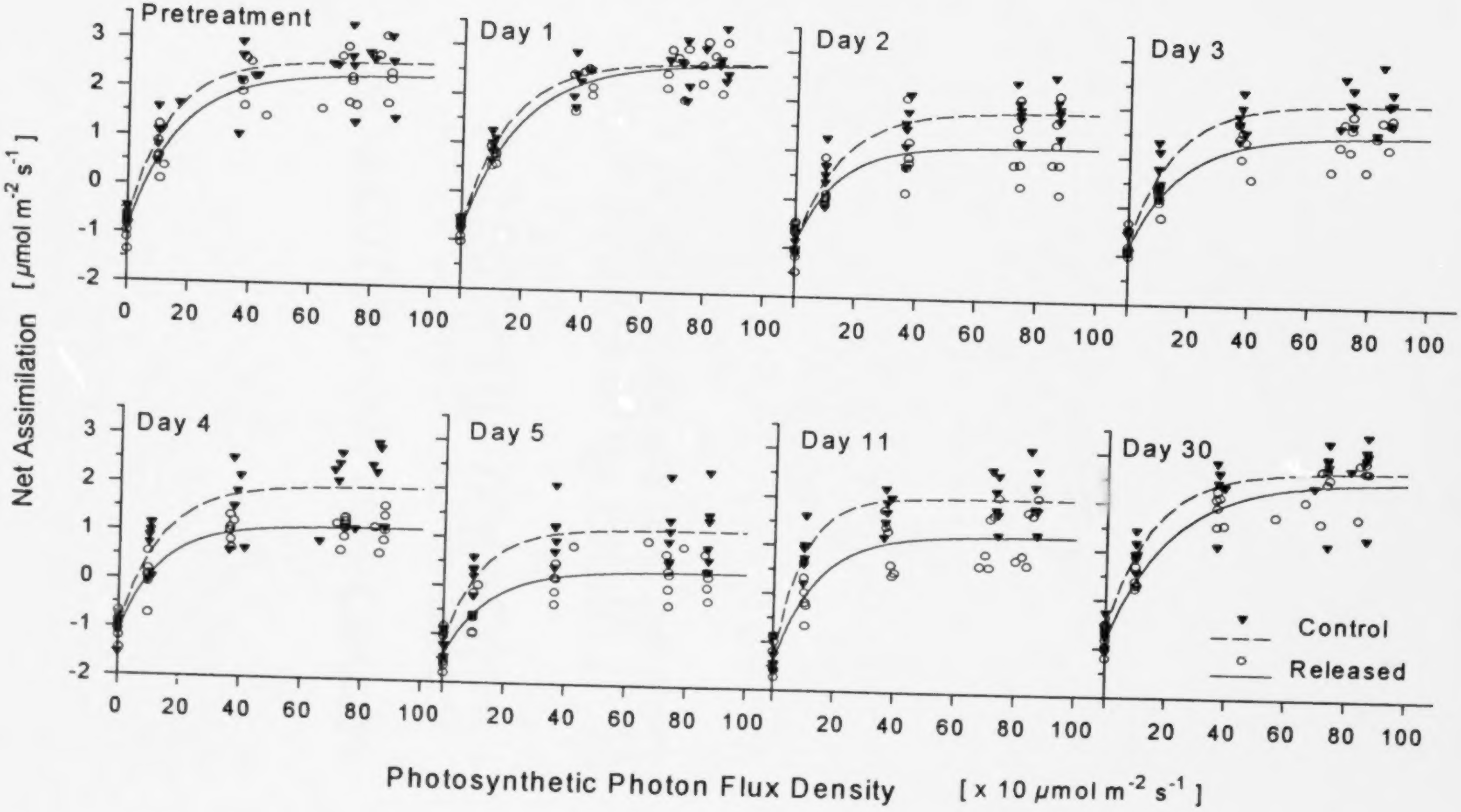

Figure 2-2. Net assimilation rate as a function of photosynthetic photon flux density in white spruce before and after overstory vegetation removal for released trees and for the controls. Best fit non-linear regression lines are also shown.

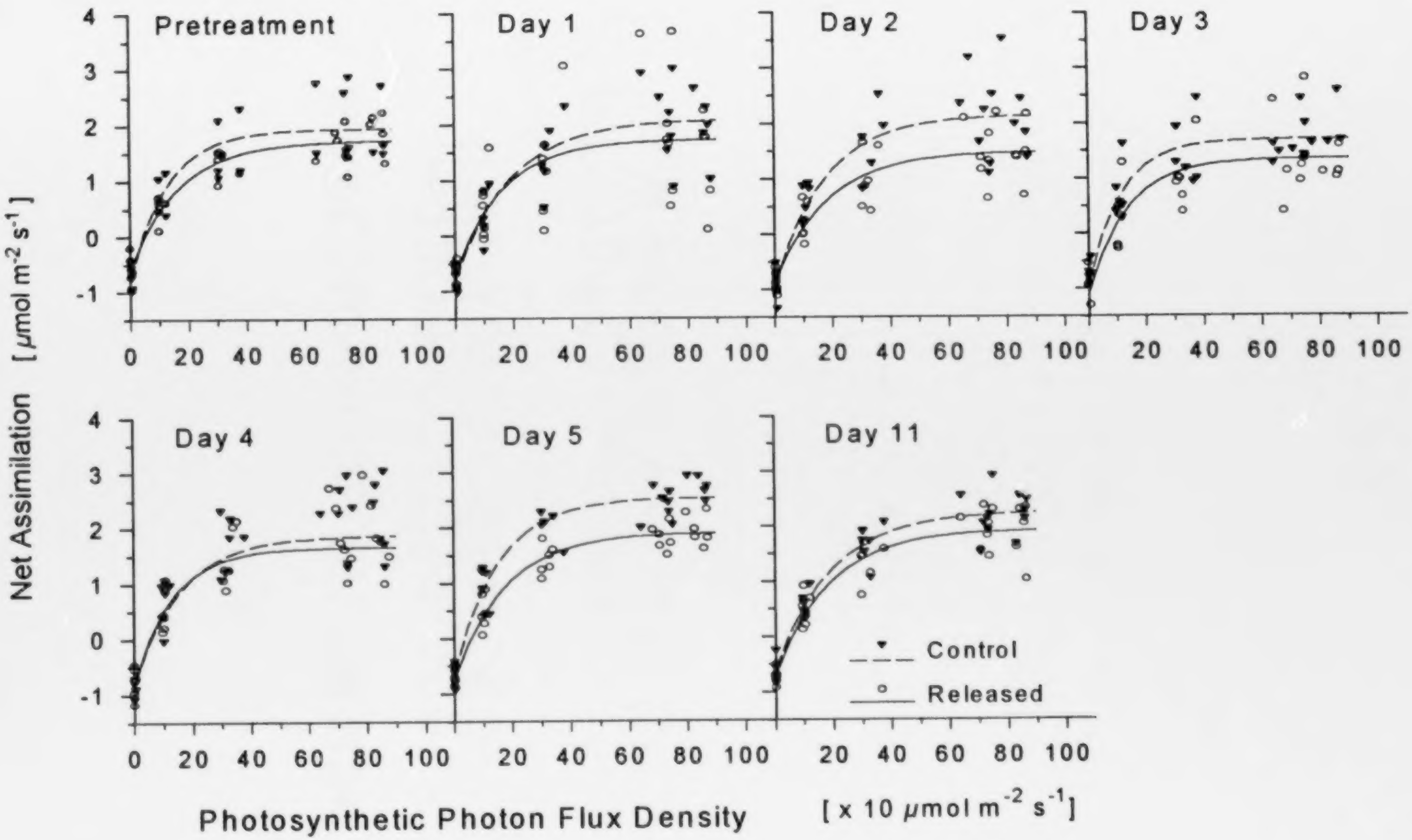

Figure 2-3. Net assimilation as a function of photosynthetic photon flux density for lodgepole pine before and after overstory vegetation removal for released trees and for control trees. Best fit non-linear regression lines are also shown.

Chapter Three

Season of release alters understory white spruce morphology and physiology

Introduction

Plant growth depends on light energy to drive photosynthesis. Light fluence rate can be tremendously variable and change over time scales from as short as seconds to as long as decades. Adaptations to physiology and/or morphology allow plants to occupy habitats characterised by very low, very high, or highly variable light levels. Physiological acclimation is usually rapid, involving changes in non-structural components such as enzymes or pigments. Numerous studies have shown that plants of many forms, have a large capacity for rapid physiological acclimation to a changed light environment (Boardman 1977; Björkman 1981). Changes in plant morphology, on the other hand, involve the production of new tissue and, as such, may occur gradually over much longer time periods. Therefore, when a plant is exposed to a permanent change in its light environment, an immediate physiological acclimation may be followed by an extended period of morphological change. Since changes in morphology will be manifest in newly produced tissue, the timing of the change in light relative to bud, leaf or shoot development, may influence the type of response and the lag time before its effects are fully expressed.

White spruce, (Picea glauca (Moench) Voss) is a shade tolerant conifer that commonly co-occurs with trembling aspen (Populus tremuloides Michx.) in mixed-wood stands of the boreal forest. In the early stages of succession, spruce may form an understory in stands with an aspen canopy, but being longer lived it will become the dominant canopy species in late successional stages (Neinstaedt and Zasada 1990). While the low light experienced by understory individuals is very different from the high light conditions of the canopy, white spruce can withstand removal of the overstory (release) and may respond with increased growth in subsequent years (Yang 1989; Navratil 1994). There is little information about the morphological changes that occur in white spruce after release or how these changes may affect tree growth. Furthermore, the role of the timing of release on changes to crown and shoot morphology has never been investigated. White spruce is an ideal species to study shoot morphological responses to timing of release because shoot growth is separated into two distinct phases.

Shoot growth in determinant species is characterised by the development of preformed tissue in the bud the first year, and the expansion of the overwintered dormant bud the next. In white spruce, bud scales begin to form in spring (June) with needle primordia initiation starting after shoot expansion is nearly completed (late July) (Owens et al. 1977). An initial rapid phase (3-6 weeks) of needle primordia initiation is followed by slower continued primordia initiation until it ceases with the onset of dormancy in late fall (October) (Pollard 1973; Owens et al. 1977). Environmental conditions during bud formation and/or shoot expansion can influence shoot development and growth (Ford 1980) and hence also the morphology of the fully expanded shoot.

Evidence from broad-leaved species suggests that changes in light environment can alter leaf anatomy, thickness, and specific leaf area (Björkman 1981) and that the developmental stage at which leaves are transferred to a different light regime, can affect the extent to which the leaf morphology is altered (Goulet and Bellefleur 1986; Eschrich et al. 1989; Sims and Pearcy 1992). In conifers, changes to needle anatomy may also be accompanied by changes in shoot morphology (needle distribution and orientation on the shoot) (Leverenz and Jarvis 1980; Greis and Kellomäki 1981). In determinant species like spruce, then, the timing of a change in light may alter needle anatomy or shoot morphology (or both) depending on when these characteristics are set.

To test how the timing of a change in light fluence rate affected morphology and physiology, understory white spruce were released (overstory removed) at different times of the year. It was hypothesised that morphologic responses of trees released in the summer (during bud development) would differ from those released during bud dormancy (fall and winter), if conditions during bud development were the most important factors determining the post-release morphology. If, on the other hand, conditions during shoot expansion controlled morphology, then spring/summer and winter/fall release treatments would result in trees with a similar morphology.

Methods and Materials

Site and Treatments

The site chosen for this study was a mixed-wood boreal forest at Carrot Creek (52°28'N, 116°49'W), 60 km south-west of Edson, Alberta. Stands in this area originated in the mid-1970s after the predominately aspen stands were pushed over, wind-rowed and aerial seeded to white spruce. The dominant overstory vegetation was 4-5 m high canopy of aspen mixed with patches of 3-4 m alder (Alnus crispa (Ait.) Pursh). Healthy sapling white spruce that were fully shaded and no more than 2 m tall were selected for study. Fifteen trees were randomly assigned to be released on each of: June 2, July 8, August 15, September 21, 1990 and 10 trees each on November 27, 1990, February 6, April 5, and June 10, 1991; hereafter referred to as Jun-90, Jul-90, Aug-90, Sep-90, Nov-90, Feb-91, Apr-91, Jun-91, respectively. Fifteen trees were also selected to serve as controls. This set of experimental trees is hereafter referred to as the "1990 release". All vegetation within a 2 m radius of a treated tree and any vegetation causing significant shade to fall on treated trees between 1000 and 1500 h was felled. The entire set of trees covered an area approximately 10 ha in size.

In the summer of 1993, a subset of the treatments was replicated in the same area to confirm the findings of the 1990 experiment, and is referred to as the "1993 release". Around ten study trees all vegetation within a 2 m radius was cleared on June 8, September 15, and November 22, 1993; ten additional controls were also established.

Crown Morphology

For all trees of the 1990 release, the following variables were measured in October 1992: growth of the terminal leader, and lateral branches in 1990, 1991 and 1992; and the total number of buds on the 1992 terminal, and the number of lateral branches on the 1991 and 1990 internodes. These data were expressed as: number of buds or branches per centimetre (branching density) and total number of buds or branches per internode. For each tree, lateral shoot growth was taken as the average of two, three-year-old first order south facing branches. For the 1993 release, the number of buds and branches on the 1992 - 1994 terminal leaders was counted and the lengths were measured to the nearest 0.5 cm in November 1994. Lateral branch lengths were measured on a single south facing three-year-old branch for the same years. To estimate changes in apical control, the ratio of the terminal leader growth to mean lateral branch growth was calculated for each of the three years of the 1990 release.

Shoot Morphology

Shoots were collected from all trees of the 1990 release in October of 1991. Two south facing two-year-old lateral branches were used to determine the number and length of needles, and shoot growth for shoots expanded in 1990 and 1991. Needle density was calculated by dividing the total number of needles by the shoot length. Shoot silhouette area was determined for each shoot by an image analysis system. For each of two images per shoot, the shoots were placed on a light table in the orientation found on the tree. In understory spruce this is easily accomplished as needles are not evenly distributed around the shoot axis; fewer needles exist on the lower portion of the shoot. The silhouette image of each shoot was digitised and its area computed by a computer. The needles were removed from the shoots and the projected leaf area (PLA) was measured as a mean of three passes through a leaf area metre (LI-3100, LiCor, Lincoln, Nebraska). To calculate total leaf area (TLA), a subsample of trees were randomly selected from each release treatment. For each tree, two subsamples of five needles each were cut in cross section at the upper, middle, and lower third of each needle. Needle area was calculated by multiplying individual needle length by mean needle circumference measured by hand digitising magnified images of each cross section. TLA was regressed against PLA for each replicate subsample. According to the test for coincident linear regression lines (Zar 1984), treatment did not significantly alter the relationship between PLA and calculated TLA within any one year. The data were pooled for all treatments within each year yielding the best fit regression lines as follows: 1990 and 1991 TLA = -0.284 + 2.855(PLA), and in 1992 TLA = 0.4465 + 2.847(PLA).

Silhouette to Total Leaf Area ratio (STAR) was calculated as the shoot silhouette area divided by the TLA predicted from the PLA of the detached needles. Since silhouette area was determined with stems perpendicular to the camera it represents values typical of solar noon. Stem area as a proportion of silhouette area was generally small and, because it was very difficult to estimate its contribution to shoot silhouette area, a correction was not made for it.

Gas Exchange

Photosynthesis was measured between 0900 and 1700 hrs on July 25 and 26, 1992, on 1991 and 1992 needles from Jun-90, Aug-90, Nov-90, Feb-91, Apr-

91 and Control trees of the 1990 release. Treatments were blocked in time on the measurement days to ensure that diurnal cycles in photosynthesis were accounted for. A portable infrared gas analyser (LCA-2, Analytical Development Co. Ltd., Hoddesdon, England) and a conifer cuvette (PLC(C)) were used for all measurements. Incoming air was dried to 2% RH and when needed, supplemental lighting was used to produce saturating light. Net assimilation (NA, μmol CO_2 m^{-2} s^{-1}) and transpiration (E, mmol H_2O m^{-2} s^{-1}) were calculated according to the equations of von Caemmerer and Farquhar (1981). Residual conductance (g_r mmol m^{-2} s^{-1}) was calculated as NA divided by internal CO_2 concentration (Jones 1985). All photosynthetic measurements were expressed on a silhouette shoot area basis to account for changes in needle distribution between 1991 and 1992 needle cohorts.

Data Analysis

The data for the year of treatment application (1990) were analysed separately from the subsequent years data since all treatments had not been applied until the spring of the second year (1991). Analysis of variance (ANOVA) was used to test for the effect of treatment in the 1990 data, and for treatment and year effects in the subsequent years' data. Contrasts were used to test specific treatment effects in the crown morphology and gas exchange variables. Dunnett's test was used to identify significant differences in means of treated relative to control tree shoot morphology variables.

Results

Crown Morphology

In the year of treatment application, released trees had significantly ($P<0.001$) more branches (Table 3-1) and a higher branch density (Fig. 3-1A) than the controls. The July-90 and Aug-90 treatments had more branches (Table 3-1), while the Jun-90, Jul-90, and Aug-90 resulted in greater branch densities than the controls (Fig. 3-1A) ($P< 0.05$). In 1991 all treatments had a greater branch density relative to the controls, but in 1992 bud density was unaffected by treatment (Table 3-2, Fig. 3-1A). Similarly, the total number of branches was higher in all treatments than the controls in 1991 ($P=0.044$), but no effect was seen bud densities in 1992 ($P=0.27$) (Table 3-1). For the 1993 release, no effect of treatment was found in either the total number of branches or in branch density in the year of treatment application (Table 3-1; Fig. 3-2A). Bud densities and total bud counts in the first year after release (1994), however, were greater in released trees than the controls ($P<0.001$, $P=0.048$ respectively) (Table 3-1, Fig. 3-2A).

In the year of treatment application (1990), no treatment effect was found in either terminal or lateral shoot growth in either release trial (Fig. 3-1 B,C, Fig. 3-2B,C). In the 1990 trial, trees release in either June or July (1990) tended to have greater leader growth in 1991 than the controls. All other treatments had leader growth similar to the controls trees in both 1991 and 1992 (Fig. 3-1B, Table 3-2). No treatment effect on leader growth was found in the 1993 release (Fig. 3-2B).

No treatment effect on lateral shoot growth was found in the year of treatment application in either the 1990 or 1993 release (Fig. 3-1C, 3-2C). In the 1990 release, the Jun-90 and Jul-90 released trees, however, had greater lateral shoot growth in 1991 than the controls did (about 2 cm). No other treated trees in 1991 and none in 1992 in the 1990 trial, as well as none in the 1993 trial, showed a response to the release treatment (Fig. 3-1C, 3-2C and Table 3-2). Leader and lateral shoot growth responses were different in the Jun-90 and Jun-91 released trees (Fig. 3-1B,C). The Jun-90 released trees generally showed increased growth in 1991, while the Jun-91 treatment showed no effect in 1992. The ratio of leader to lateral length (a measure of apical control) did not differ significantly by year or treatment in either the 1990 or 1993 release trials (data not shown).

Shoot Morphology

All shoot morphological variables were similar to controls in the year of release, but treatment effects were seen in the first year after release (Fig. 3-3). Needle lengths were generally shorter in released trees in 1991, particularly in trees cleared prior to November (Jun-90, Jul-90, Sept-90) (Fig. 3-3A, Table 3-3). Overall, values for STAR decreased from 1990 to 1991, but in 1991 released trees (except Jun-90, Jul-90 and Jun-91) had lower values than controls (Fig. 3-3B, Table 3-3). Needle densities were greater in treated trees than in controls in 1991, however, this was only statistically significant in June and September release dates (Fig. 3-3C). Greater needle densities in 1991 in most treatments were associated with reduced lateral branch length in 1991 (compared to 1990) (Fig. 3-1C). Specific leaf area (cm^2/ gm dry wt.) as well as mean needle circumference were unchanged by release treatments in either the year of release or the following year (data not shown).

Gas Exchange

All needles which flushed in 1991 or 1992 in released trees had significantly higher NA and E than did the controls (Fig. 3-4A,B, Table 3-4). In 1991, pre-dormancy released trees (Jun-90 and Aug-90) and the post-dormancy released trees (Nov-90, Feb-91and Apr-91) did not differ in NA rates (Table 3-4). Yet in the 1992 formed tissue, post-dormancy released trees had significantly higher NA (60%) than the pre-dormancy trees and almost three times greater than the controls (Fig. 3-4A, Table 3-4). The pattern for transpiration mirrored that of net assimilation (Fig. 3-4B). Released tree STAR values for shoots used for gas exchange were lower than controls in 1991 (as noted before) but remained so in 1992. Analysis of foliar nitrogen concentrations of the 1991 and 1992 gas exchange needles in June 1990, April 1991, and controls, showed no differences between treatments in either year. However, in both these release treatments, the 1992 needle cohort nitrogen concentrations were greater than those found in the 1991 cohort (1.11% vs 0.98%, P=0.024).

Discussion

Crown Morphology

The largest single change to crown architecture was the significant increase in the total number and density of branches in 1990 in the spring-released trees, and in all treatments in 1991. In both years, shoots developed from buds set in the shaded understory produced significantly more branches than did the controls. This indicates that the number of lateral branch buds produced in the shade in was higher than the number of branches that remained at end of the growing season. The conditions after release did not alter bud production in the 1992 leaders, which would also suggest that lateral bud numbers may be insensitive to prevailing environmental conditions, but that the number of surviving branches is. However, the data from the 1993 release indicate that bud production after release was higher than in the controls. Thus the control over bud and branch production are likely a function of conditions before and after release. The release treatments may have altered branch development through the provision of higher carbohydrate levels made available from enhanced photosynthetic rates in released trees.

The 1990 release trial showed a trend for lower branch densities in the Aug-90 and Sept-90 trees relative to the Nov-90 released trees, suggesting a detrimental effect of late fall release. To confirm these findings a scaled-down replicate was installed in 1993. It failed to show a similar reduction in bud density in fall released trees, however. Other similar inconsistencies were found in several responses to release within, and between release trials. For example, increased terminal and lateral shoot length was found in Jun-90 and Jul-90 trees in 1991, but was not found in the Jun-91 trees one year after their release (1992), nor was it found in the June released trees of the 1993 trial. The crown responses to environmental changes resulting from the release treatments appear to be a function of many factors such that treatment effects appear inconsistent.

By the fall of the year of treatment application, no change in terminal or lateral shoot length was found which suggests that these characteristics were unaffected by conditions during bud expansion, but rather are set by conditions during the development of the bud the summer prior to release. Shoot growth is largely the result of expansion of preformed cells that were overwintered in the bud (Owens et al. 1977). Shoot growth may therefore, be highly variable from year to year, depending on climatic conditions during bud development and shoot expansion, as well as tree-to-tree variation in response to these climatic conditions. As understory conditions prevailed in all treatments during the development of the buds that flushed in year of treatment (1990), that year's shoot growth was expected to be similar in released and control trees. However, shoots that expanded in 1991 in the Jun-90 and Jul-90 trees (from buds set in the open) would be expected to differ from the remaining trees in which the buds had been set in the understory (in 1990). While greater leader and lateral growth the year after treatment was noted in Jun-90 and Jul-90 trees, this response was not found in trees that set bud and flushed in similar conditions in the following year (1991). Although individual tree shoot growth may be highly variable, the ratio of terminal-to-lateral shoot growth can be quite sensitive to prevailing light conditions (Oliver and Larson 1990).

There was no significant change in terminal-to-lateral shoot ratios in any trees regardless of time of release. Furthermore, no difference in this ratio was detected between released or control trees. A change in relative growth between terminals and laterals shoots when light conditions change has been found in other spruce species (Leverenz and Jarvis 1980; Greis and Kellomäki 1981). Although classed as a shade-tolerant tree (Neinstaedt and Zasada 1990), understory white spruce do not have distinctively flattened crowns as due the very shade tolerant balsam fir (Abies balsamea (L.) Mill) found scattered in this area (personal observation). The maintenance of height growth in the understory may serve to maximise light interception by ensuring that an individual's crown stays above other understory vegetation.

A clear result of the release treatments, regardless of time of release, is the positive effect on whole plant carbon gain. Greater carbon gain may occur as the result of an increased rate of photosynthesis, and/or an increase in the photosynthetic leaf area receiving high fluence light.

Photosynthetic Potential

This study showed clear evidence of a large increase in photosynthetic capacity in all needles produced one and two years after release. Net assimilation rates after release were more than double that of controls in needles flushed the year after release and nearly triple in those produce in the second year. Higher net assimilation rates one year after release were also found by Lieffers et al. (1993), however the large increase in second year photosynthetic rate illustrates that acclimation may continue for some time after release. The lack of difference in photosynthetic rates in needles expanded in 1991 from buds set in open conditions (Jun-90 and Aug-90) compared to those set in the shade (Nov-90, Feb-

90 and Apr-91), may be the result of limited acclimation of the needle anatomy after release. Physiological acclimation to high light conditions should have occurred in both groups' needles since by July when the photosynthesis measurements were made, all needles would have been exposed to a summer of full sunlight. The only differences between these groups would be in the conditions under which bud formation occurred. Further investigations are needed to establish the extent and nature of changes in needle anatomy in response to release, although this data indicate the possibility that sun type needles may be formed from buds that develop either under shade or full sun conditions.

The large difference in photosynthetic net assimilation rates in second year needles (1992) in trees released prior to bud set (Jun-90 and Aug-90,-- pre-dormancy release), versus those released after buds set (Nov-90, Feb-91, and Apr-91. -- post-dormancy release), was unanticipated. It was expected that by the second year after release, all treatments would have equal adjustments to their physiology and morphology producing essentially identical photosynthetic rates. All buds were formed, and subsequently flushed, under similar environmental conditions so the effect of treatment should have been the same in all released trees. Foliar nitrogen concentrations were higher in the 1992 tissue relative to the 1991 needles, however, this was true in both June and April release treatments. Higher foliar nitrogen concentrations, therefore, cannot explain the difference in photosynthetic rates between pre-dormancy and post-dormancy released trees. Two hypotheses are offered to explain these results.

Following the initial release treatment, no further vegetation control was applied to these trees. In the pre-dormancy released trees, two growing seasons had elapsed between treatment application and photosynthesis measurements thus the competing vegetation had this time to re-establish. The post-dormancy treatments, in contrast, had a single year for vegetation re-establishment. Although the vegetation had not re-developed sufficiently to cause significant shade, it is possible that greater below-ground competition resulted in poorer photosynthetic performance in the former set of trees. The second explanation lies in the way in which the needles were arranged on the shoots. STAR showed an inverse trend to that of net assimilation, with high net assimilation rates associated with low STAR values. A reduced STAR indicates more total leaf area per unit of silhouette area. Under high light, a considerable amount of needle surface area may be illuminated by diffuse radiation. Thus when the photosynthetic rate is expressed on a shoot silhouette area basis, it will be greater than when expressed on a total leaf area basis, and will exaggerate the assimilation rate of trees with low a STAR (post-dormancy released trees). Small differences in STAR were noted between pre- and post-dormancy released trees which could not fully account for the large difference between these two groups' assimilation rates.

The higher per-unit-area photosynthetic rate of released trees over the controls was also accompanied by an increase in photosynthetic leaf area. A significant greater number of branch the first year after release was found in both release trials. Higher needle densities in released trees over control trees were found despite the similar length of shoots indicating an increase in absolute needle numbers. Higher photosynthetic area in released trees in conjunction with greater photosynthetic rates, should greatly enhance their ability to assimilate carbon.

The increase in shoot needle density was accompanied by a reduction in STAR, indicating a greater needle packing, particularly in fall and winter released trees. STAR values near unity are found in shoots that have the majority of their needles illuminated by direct beam radiation. Lower STAR values indicate shoots with needles inclined from the horizontal and/or with considerable needle self-shading. Changes to shoot STAR may be beneficial to plant performance in two ways. A vertical needle orientation will allow greater needle packing without a significant reduction in photosynthesis under conditions of high fluence light (Carter and Smith 1985). Secondly, vertical needle orientation will produce an even radiation load over the course of a day by reducing mid-day interception yet increasing interception at low solar angles (Ehleringer and Werk 1983). The maintenance of uniform light levels will maximise daily shoot photosynthetic performance and minimise extreme needle temperatures. It may also reduce the potential for photoinhibition (Ehleringer and Cooper 1992) which can occur in plants subjected to high fluence light (Ögen and Rosenqvist 1992).

In the Jun-90 and July-90 trees, a higher needle density was not associated with a reduction in STAR, but rather was associated with shorter needles. It appears that shoots developed in the open have a similar amount of leaf area for light interception, but this area is displayed either in densely packed short needles with minimal self-shading (Jun-90 and Jul-90) or in densely packed shoots with longer needles (all others). The increase in the photosynthetic leaf area, the placement of new shoots at branch tips which will be under photosynthetically saturating light levels, and the inherently greater photosynthetic capacity of the new tissue will greatly increase whole plant carbon assimilation potential.

Despite this evidence suggesting a potential for greatly increased carbon gain, there was little evidence of greater diameter growth in shoots formed after release. It is likely that the increased branch and needle production acted as large sinks for photosynthates and that increased root growth would also compete for available energy. Allocation away from roots under shaded conditions commonly occurs (Björkman 1981; Givnish 1988) and results in low root:shoot ratios. Such an imbalance in favour of above-ground biomass may not be detrimental in the understory. In open conditions, however, increased vapour pressure deficits (Oke 1987) and higher nutrient and water demands from the greater needle area would require a larger below-ground root network. It is likely that the small above ground increase in height and diameter growth (relative to the unreleased controls) is indicative of higher carbohydrate demands for the production of new roots and needles, rather than a poor whole-plant carbon status. The lack of evidence of increased above-ground growth noted here is likely a short-term response. White spruce has been shown to respond with greater diameter growth 3-5 years after release (Johnson 1986; Navratil et al. 1994).

The timing of release did not appear to have any negative effect on shoot growth. Release prior to bud flush facilitated the development a greater number of shoots in the year of release than in control trees. Release significantly increased the whole plant carbon assimilation potential through increasing the photosynthetic rates, and producing more leaf area oriented to optimise the interception of light.

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Table 3-1. Total number of branches and buds per internode measured in October of 1992 or 1994, on trees released over several months between June 1990 and June 1991 or June and November 1992. Means ±SE are shown, n ranges from 10 to 15.

Time of Release	1990 Release			1993 Release	
	Branches		Buds	Branches	Buds
	1990	1991	1992	1993	1994
Jun-90	10.8 ±4.1	11.3 ±2.0	18.2 ±2.2	8.3 ±1.1	10.9 ±1.0
Jul-90	16.1 ±6.4	8.7 ±1.0	17.4 ±2.0	--[1] --	-- --
Aug-90	13.4 ±5.8	6.7 ±0.9	14.0 ±2.0	-- --	-- --
Sept-90	11.7 ±5.1	5.7 ±1.0	14.4 ±2.3	10.0 ±1.3	10.1 ±1.8
Nov-90	10.5[2] ±5.2	8.9 ±1.4	14.8 ±2.6	6.7 ±1.0	8.6 ±1.0
Feb-91	9.7[2] ±4.1	8.1 ±1.6	12.7 ±1.2	-- --	-- --
Apr-91	8.4[2] ±4.8	6.9 ±0.9	11.0 ±2.3	-- --	-- --
Jun-91	7.8[2] ±3.6	5.7 ±0.7	12.9 ±1.8	-- --	-- --
Cont	7.4 ±3.3	4.3 ±0.8	12.6 ±1.6	6.9 ±1.1	6.9 ±1.2

[1] Treatments not applied

[2] Pre-release measures

Table 3-2. 1990 release trial ANOVA table for treatment and year effects on crown morphology variables for sapling white spruce released from overstory competition in eight months between June 1990 and June 1991. Probabilities associated with specified contrasts are also given. Treatment abbreviations as in text.

Variable	Source of Variation	DF	F Value	Prob. > F
Terminal Leader Branch Density				
	Year	1	8.80	0.003
	Treatment	8	2.30	0.022
	Year x Treatment	8	1.06	0.395
	Treated vs Control in 1991	1	15.88	<0.001
	Treated vs Control in 1992	1	0.97	0.326
Terminal Shoot Length				
	Year	1	23.60	<0.001
	Treatment	8	2.78	0.006
	Year x Treatment	8	0.26	0.978
	Jun90 & Jul90 vs Control in 1991	1	3.11	0.079
	Jun90 & Jul90 vs Control in 1992	1	4.02	0.046
	Aug90 thru Jun91 vs Control in 1991	1	0.10	0.753
	Aug90 thru Jun91 vs Control in 1992	1	0.28	0.595
Lateral Shoot Length				
	Year	1	13.96	<0.001
	Treatment	8	2.58	0.010
	Year x Treatment	8	0.89	0.522
	Jun90 & Jul90 vs Control in 1991	1	6.09	0.014
	Aug90 thru Jun91 vs Control in 1991	1	0.59	0.443
	Treated vs Control in 1992	1	0.04	0.833

Table 3-3. ANOVA table for effects of season of release on shoot morphology variables of white spruce saplings measured one year after release. Probabilities for selected contrasts are also given.

Variable	Source of Variation	DF	F Value	Prob. > F
Needle Length				
	Treatment[1]	8	5.61	<0.001
	Treated vs Control	1	12.77	<0.001
STAR				
	Treatment	8	2.45	0.023
	Treated vs Control	1	12.19	<0.001
Needle Density				
	Treatment	8	2.17	0.040
	Treated vs Control	1	5.52	0.022

[1] Release treatments were applied at seven times over the course of a year.

Table 3-4. ANOVA table for effects on photosynthetic variables in sapling white spruce released from overstory vegetation. Gas exchange was measured in July of 1992 on current (1992) and one-year-old (1991) shoots of trees released from overstory vegetation between June 1990 and June 1991. Probabilities associated with specified contrasts are also given.

Variable	Source of Variation	DF	F Value	Prob. > F
Net Assimilation				
	Year	1	17.16	<0.001
	Treatment	8	19.86	<0.001
	Year x Treatment	8	12.06	<0.001
	PrD[1] vs PoD[2] in 1991	1	1.56	0.214
	PrD vs PoD in 1992	1	26.59	<0.001
	Treated vs Control in 1991	1	7.56	0.007
	Treated vs Control in 1992	1	24.38	<0.001
Transpiration				
	Year	1	9.07	0.003
	Treatment	8	15.40	<0.001
	Year x Treatment	8	8.25	<0.001
	PrD vs PoD in 1991	1	2.71	0.103
	PrD vs PoD in 1992	1	14.85	<0.001
	Treated vs Control in 1991	1	9.34	0.003
	Treated vs Control in 1992	1	18.36	<0.001

[1] Pre-Dormancy released trees = Jun90 and Aug90.

[2] Post-Dormancy released trees = Nov90, Feb91, and Apr91.

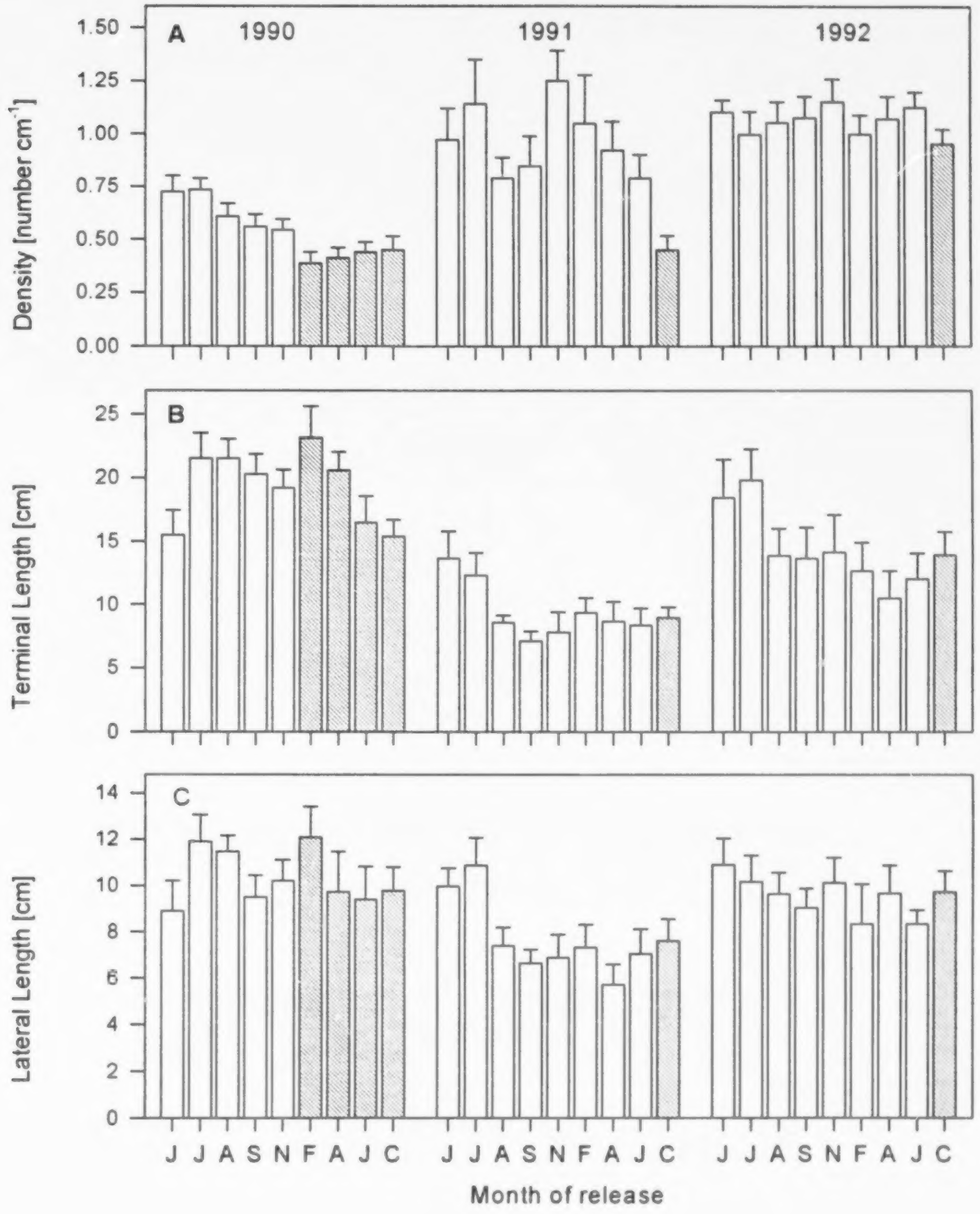

Figure 3-1. Mean terminal leader branch (1990-91) or bud (1992) density (A), terminal leader length (B) and lateral branch length(C) measured in October 1993 in sapling white spruce released from a hardwood overstory. Release treatments were applied from June of 1990 ('J' at left extreme) to June 1991 ('J' at right). Unreleased trees at time of measurement are shown with hatched bars, 'C' are the control trees. Vertical bars indicate 1 SE, n ranges from 10-15.

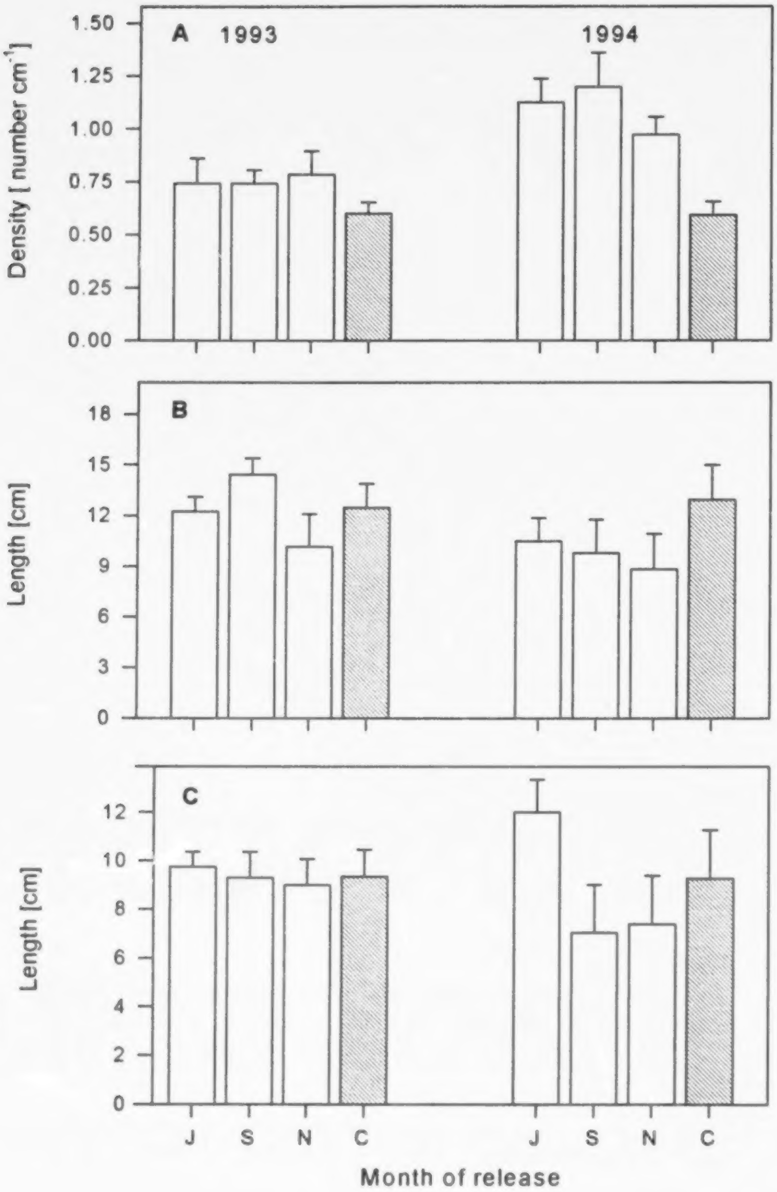

Figure 3-2. Mean branch (1993) or bud (1994) density (A), terminal leader length (B), and lateral branch length (C) of sapling white spruce in the year of, and one year after release from a hardwood overstory. Release treatments were applied in June, September, and November 1993. Control trees 'c' shown with hatched bars; vertical bars indicate 1 SE.

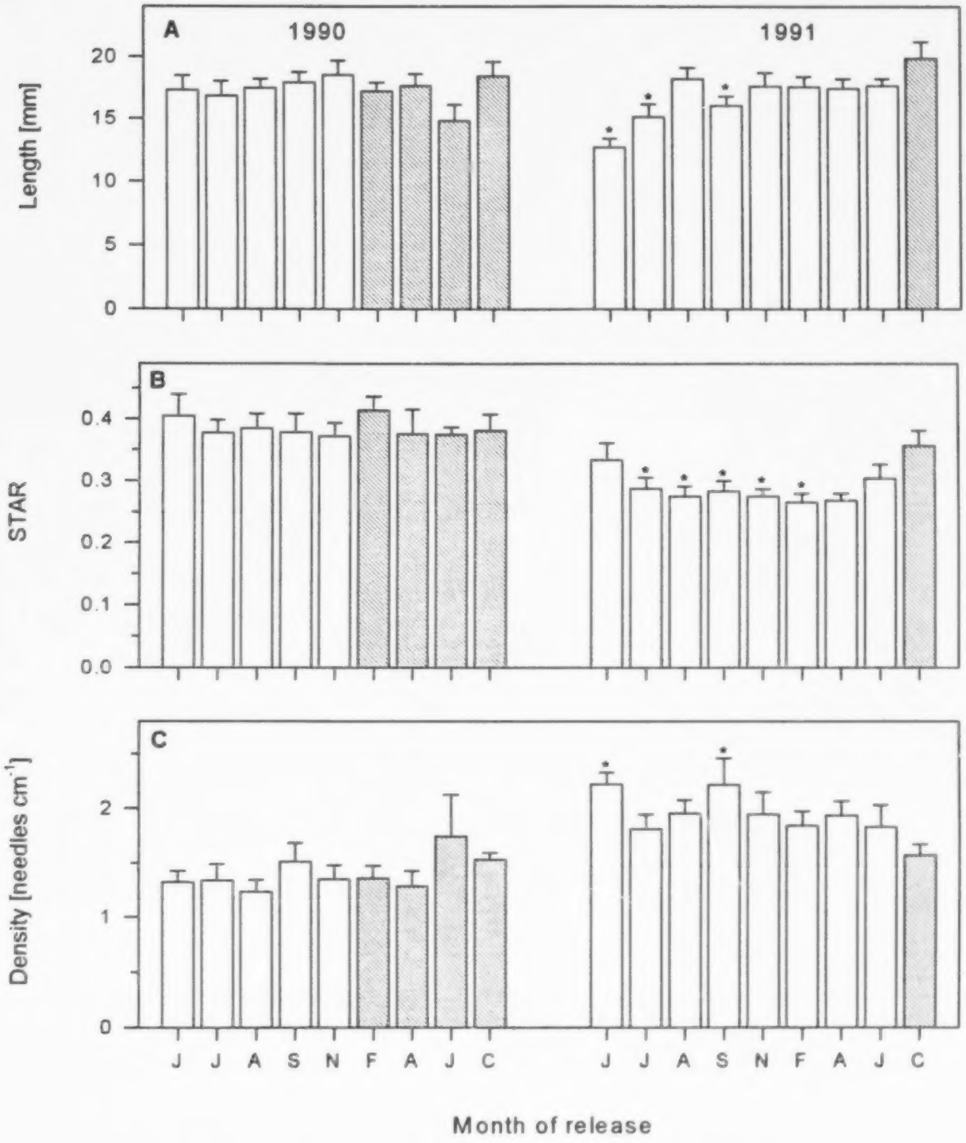

Figure 3-3. Mean needle length (A), Silhouette to Total leaf Area Ratio (STAR) (B) and needle density (C) in sapling white spruce trees released from overstory vegetation. Release treatments were carried out over a one year period from June 1990 to June 1991. Hatched bars indicate measurement on unreleased trees, 'C' indicate control trees. Vertical bars indicate 1 SE, n =10. '*' indicate treatment means significantly different from control ($P<0.05$) determined by Dunnett's test.

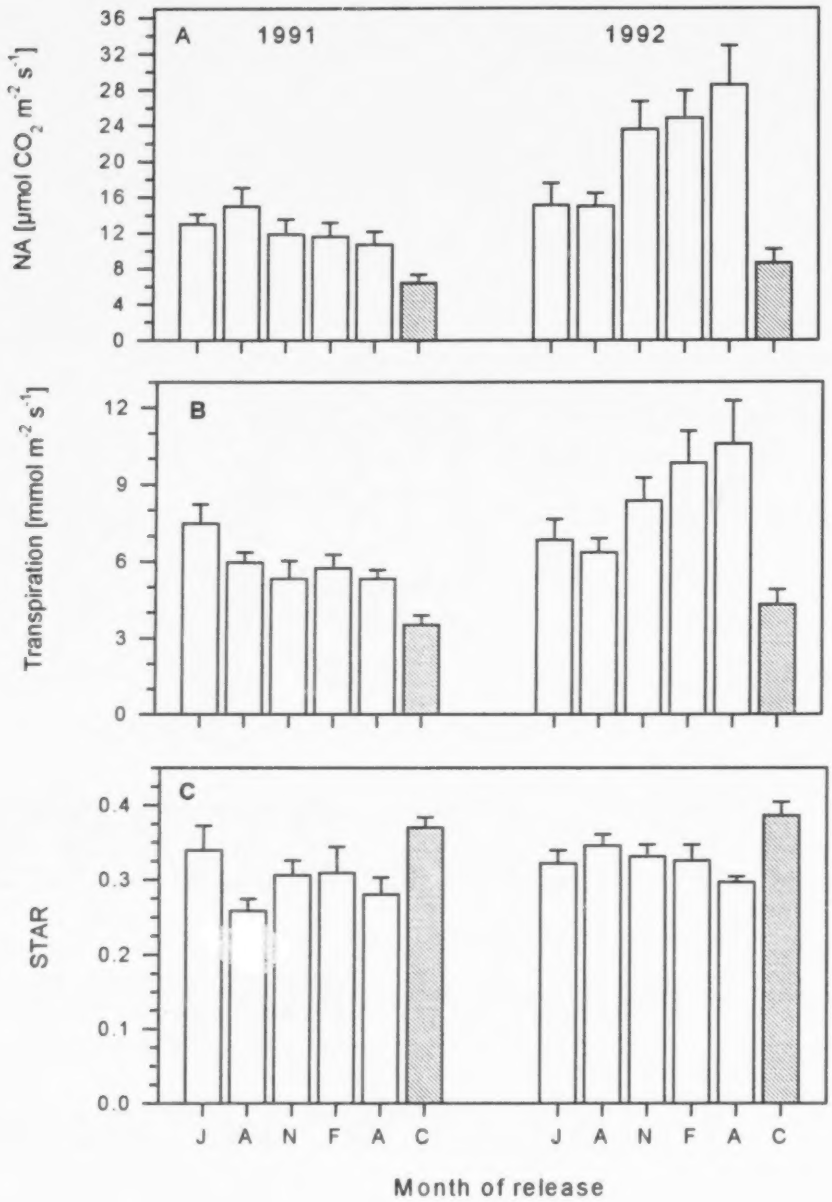

Figure 3-4. Mean net assimilation rate (A), transpiration rate (B) and STAR (C) of current (1992) and one-year-old (1991) shoots measured in July 1992 on sapling white spruce trees released from overstory vegetation in June 'J', August 'A', and November 'N'of 1990, and February 'F'and April 'A'of 1991. Control tree 'C' means are shown by hatched bars; vertical bars indicate 1 SE, n=10.

Chapter Four

A boreal forest grass with an open meadow photosynthetic strategy

Introduction

Differences in photosynthetic properties between sun-grown and shade-grown plants, and within plant differences, between sun and shade leaves, have been noted in numerous species (Björkman 1981). Species that are able to maintain themselves in an understory, yet are also able to dominate in open sites, would be expected to have shade and sun phenotypes, each acclimated to their respective light environment. Shade phenotypes (plants or leaves) typically have low respiration rates, low light saturated photosynthetic rates, as well as different leaf anatomy and organisation of sub-cellular photosynthetic constituents (Björkman 1981). Understory environments are characterised by light of low photon flux density (PPFD), however it may be punctuated by short, high PPFD periods (sunflecks) or more protracted periods of sun or shade resulting from mutual shading between leaves or passing clouds. Periods of high PPFD can be crucial for understory plants photosynthesis (Chazdon and Pearcy 1991). Under fluctuating light levels, the synchrony between stomatal and biochemical limitations to photosynthesis can have considerable impact on plant carbon assimilation and water loss.

Species differ in how stomatal conductance of water vapour (g_s) and net assimilation (NA) respond to variable light (Woods and Turner 1971; Knapp and Smith 1989,1990). "Tracking response", where g_s closely follows changes in NA and light, is typical of herbaceous species; the "nontracking response", characterised by relatively steady but low g_s over a large range of NA and light, is typical of many woody species (Knapp and Smith 1989, 1990). Stomatal conductance synchronised with the changing light conditions (tracking) should reduce water loss during shade periods, but will also reduce carbon gain after the return of high PPFD, particularly in plants with stomata slow to respond. In many woody and herbaceous species, the rapidity of stomatal opening and closing differs (Woods and Turner 1971; Fay and Knapp 1993) which may alter the trade-off between water loss and carbon gain. The alternative strategy of relatively constant g_s under fluctuating NA and light may increase water loss relative to carbon gain under shade, but should increase carbon gain during the transition from shade to sun (Knapp and Smith 1990).

Calamagrostis canadensis (Michx (Beauv.)) (blue-joint or marsh reed grass) is commonly found in mixed-wood forests, open uplands, and wet sites across northern North America (Hitchcock and Chase 1971). Though existing on a wide range of habitats (Haeussler et al. 1990), its best growth is on moist, nutrient-rich open sites (Mueller-Dombois and Sims 1966; Laughlin et al. 1984). Little is known about the ecophysiology of C. canadensis, although its importance as a competitor with regenerating conifers has lead to the development of strategies for its control (see review by Lieffers et al. 1993). Initial field investigations into Calamagrostis canadensis photosynthetic response to light, indicated no difference between open-grown and understory plants and also indicated very slow stomatal response to variable light levels. In order to further the understanding of the photosynthetic strategy of C. canadensis, controlled environment studies were carried out to investigate the photosynthetic light response of sun- and shade-grown plants and to characterise the nature of the stomatal response to variable light.

Materials and Methods

Light Response Curve Experiment

Established greenhouse grown C. canadensis sods, planted from randomly collected seed, were split into 18 portions and tops were clipped to ground level.

Each sod was planted in a single pot in heavy loam. Nine pots were randomly selected to be sun plants and were grown outside in full sun from May to August; the remaining nine were grown under shade frames immediately adjacent to the sun plants for the same time period. Shade frames, constructed of two layers of black fibreglass screen, reduced ambient sun light to 30% of full light - a level typical of mature aspen-dominated stands (Lieffers and Stadt 1994). Plants were fertilised twice weekly with 20-20-20 NPK and watered daily.

The second and third youngest blades on four randomly selected plants each from sun and shade treatments were used to measure photosynthesis. An open system, portable infra-red gas analyser (IRGA) (LCA2 and LCA3, Analytical Development Co. Ltd, Hoddesdon, England) and a conifer cuvette (PLC(C)) were used to measure gas exchange at different PPFDs. Incoming relative humidity was maintained at 30% and leaf temperature at 22.5 °C (±0.5). Light was supplied by a 500 W, halogen flood lamp filtered through a flowing water bath providing uniform light over the width of the leaf chamber. Light levels were controlled by adjusting the height of the lamp in conjunction with neutral density filters. Six light levels were used: 30, 75, 150, 250, 400, and 1000 μmol m^{-2} s^{-1}; in addition, one dark (respiration) measurement was made after a fifteen-minute dark acclimation period. The PPFD was measured inside the leaf chamber at the position of the blade with a quantum sensor (LI-190S, Lambda Instruments, Lincoln, Nebraska). Light was increased following a period of darkness, and at each incremental increase 15 minutes were allowed to establish a new steady state equilibrium. Preliminary trials indicated that little significant change in photosynthetic rate occurred after this time interval.

For each treatment group (sun and shade) the data were fit to the monomolecular curve (Causton and Dale 1990) by least squares iterative non-linear regression in order to model the photosynthesis rate relationship to the supplied PPFD. A test for coincidence of regression lines was used to analyse the differences between sun and shade plant light response curves (Potvin et al. 1990). Photosynthetic light compensation point and dark respiration rate were calculated from the modelled light response curve for each plant (Causton and Dale 1990). Tests for significant differences in these variables between sun and shade plants were made using one-way analysis of variance.

Stomatal Response to Variable Light Experiment

Four-month-old greenhouse-grown plants, originating from randomly collected seed, were used to determine the response of C. canadensis to cycles of high and low PPFDs. The plants were grown under PPFDs that ranged from 50 - 300 μmol m^{-2} s^{-1}supplied from natural sunlight and supplemental artificial lighting. The greenhouse daytime temperature was 25 °C with a 22 °C night temperature. Plants were regularly watered and fertilised bi-weekly (20-20-20 NPK). For two hours prior to measurement, the plants were placed in a growth chamber with supplemental lights bringing the photosynthetically active radiation to 750 μmol m^{-2} s^{-1}. This was done to fully induce the biochemical components of the photosynthetic system and thus ensure that all plants within the pots were at a similar physiological state. The two youngest, fully expanded blades were used to measure the time sequence of photosynthesis at saturating light of 615 μmol m^{-2} s^{-1} (hereafter referred to as "high light") alternately with near compensating light of 33 μmol m^{-2} s^{-1} (hereafter referred to as "low light"). The light was produced by a 39 watt, 12 volt quartz halogen lamp, (Phillips, MR-16 SQ) and PPFD near the light compensation point was produced with neutral density filters. Photosynthesis was measured with a portable IRGA (LCA3) using a broad leaf cuvette (PLC(B)). The small volume of this chamber (16 cm^3) and the tubing down-stream of the leaf chamber (13 cm^3), in conjunction with a flow rate of 400 ml min^{-1}, reduced the time lag between the readings of the humidity sensor in the cuvette and CO_2

analysis of the IRGA, to less than 5 seconds. Since this lag was very short relative to the stomatal response, a correction was not made for it. In-going humidity was controlled at 30% RH and leaf temperature was measured with a thermistor appressed to the underside of a blade. The maximum difference in leaf temperature between high and low light was 2 °C.

Measurements were taken every 30 seconds for the first three minutes after a change in light level, and then at one minute intervals until the next change. A total of four plants were measured, with each subjected to three back-to-back cycles of 12 minutes high light followed by immediate decrease to low light for 8 minutes. A steady state was established after 12-15 minutes high light, while 8 minutes low light was used to re-establish a steady rate of net assimilation under the low light. The aim was to determine the time course of stomatal opening and closing immediately after a steady state equilibrium had been re-established.

Two methods were used to describe the rate of change in stomatal conductance following an increase/decrease in fluence rate of incident light. First, an averaged rate of change in g_s was estimated by regressing g_s against the time since a change in light. This was done only for the linear portion of the response curve that accounted for the mid-80% of the final steady-state level (Assmann and Grantz 1990). This slope was calculated for each high/low light cycle for each of the four plants. Second, a new variable was created by subtracting the conductance at each measurement period after an abrupt change in light, from the steady-state value achieved prior to the change. The data were fit to a sigmoidal function (the Gompertz model) to better describe the nature of the time response of the stomata to the change in light level. For each plant, pooled data from the three high-to-low light transition phases were fit to a decreasing form of the Gompertz model. Likewise the pooled data from the two low-to-high light transition phases were used to fit an increasing form of the model using a least squares iterative non-linear curve fitting routine. Characterisation of the increase in NA after the onset of high light was made with pooled data fit to an increasing form of the model for each plant. Using this non-linear model, the nature of the full range in response of g_s to variable light was more accurately described.

The Gompertz model allows for non-zero asymptotes, can be asymmetric about its inflection point, has good parameter estimation properties, and initial parameter estimates are easily obtained (Ratkowsky 1990). The general form of the model is:

$$g_s = a + b\exp\left[-\exp^{(c - d\tau)}\right]$$

where a is the lower asymptote, b is the difference between the lower and upper asymptotes, c and d are additional parameters controlling shape and τ is the time since an abrupt change in light fluence. From the Gompertz model, the time to reach 20% and 80% of the final equilibrium response and the slope at the inflection point (maximal rate of change) were calculated for each plant. A paired T-test was used to test for differences between opening and closing responses in the absolute value of the slope of the stomatal opening and closing responses, and in time taken to reach 20% and 80% of maximum response.

For both experiments, gas exchange variables were expressed on a projected leaf area basis. Net assimilation (NA, μmol CO_2 m^{-2} s^{-1}), stomatal conductance to water vapour (g_s, mmol m^{-2} s^{-1}) and CO_2 (g_c, mmol m^{-2} s^{-1}) were calculated according to the equations of von Caemmerer and Farquhar (1981).

Results

Sun and shade plants had similar photosynthetic responses to light (Fig. 4-1a). Test of coincident regression lines indicated the responses as a whole did not differ ($P=0.08$, $F_{4,27} = 2.318$). From the modelled photosynthetic light response curves, dark respiration rates were significantly lower ($F_{1,8} = 21.27$, $P<0.002$) in shade plants (1.3 ± 0.1 SE μmol m^{-2} s^{-1}) than in sun plants (1.9 ±0.08 SE μmol m^{-2} s^{-1}) as were their light compensation points ($F_{1,8} = 15.28$, $P<0.005$) (15.3 ±0.9 versus 31.5 ±3.4 SE μmol m^{-2} s^{-1} respectively). Stomatal conductance to carbon dioxide was higher in shade relative to sun plants at all light levels (Fig. 4-1b). The initial field findings of the lack of sun- and shade-plant difference in overall photosynthetic response to light (data not shown) were confirmed by the present study.

Alternating high and low light induced cyclical changes in both g_s and NA (Fig. 4-2). Rates of change in g_s differed between transition from high to low light ("closing") and low to high light ("opening"). While the closing response was immediate (Fig. 4-2; 4-3a), the opening response was marked by a 1-2 minute time lag between the onset of high light and an increase in g_s (Fig. 4-3b). The observed time lag in opening was reflected in the significantly longer time taken to achieve 20% of the final equilibrium g_s, during opening relative to closing (Table 4-1). However, the average rate of opening over the linear portion of the g_s response curve was greater than the closing rate (Table 4-1). The maximum rate of stomatal opening was also greater than the closing rate, as shown by steeper slope at the inflection point in the modelled response (Table 4-1). The faster rate of stomatal opening reduced the effect of the time lag in the opening response. As a result, the time taken to achieve 80% of maximal response (either opening or closing) did not differ between high-to-low or low-to-high light changes (Table 4-1).

With the onset of low light, NA dropped immediately and a short (1-2 min.) phase of negative assimilation was observed before a new equilibrium was established just above the compensation point (Fig. 4-2). The resumption of high light initiated an immediate rise in NA without a lag as was found in g_s response (Fig 4-3c). Thus although it took on average 2.4 min. to achieve 20% of maximum g_s response after the onset of high light, the NA response, after this same time interval, was 49% of its final equilibrium rate.

Discussion

Higher light saturated photosynthetic rates in open grown versus understory plants have been noted in numerous species (Boardman 1977; Björkman 1981). For this reason the similarity in form of the photosynthetic light response curves in both open- grown and understory plants in our preliminary field trials was not expected, neither was the corroboration of that finding in the controlled shade- and sun-grown plants. Pierson et al. (1990), also found that Bromus tectorum, when grown under varying shade regimes did not have an altered photosynthetic response to light. It is possible that the development of shade leaves may not occur in C. canadensis unless incident PPFD is even less than that supplied in this experiment, or it may be that sun and shade leaves are not formed in this species. The latter explanation appears more likely given the lack of sun and shade differences found both in this controlled study and in naturally growing understory and open-grown plants.

The low respiration rates will enable shade plants of C. canadensis to balance respiratory carbon demands with photosynthetic carbon assimilation under low PPFD. If the additional carbon costs of tissue production and maintenance are included, then the 'ecological' light compensation point (Givnish 1988), will be slightly higher than the instantaneous compensation point measured here. However, given that the mean shade-plant light compensation point (15 μmol m^{-2} s^{-1}) was less than 5% of mid-summer light under an aspen dominated mixed-wood canopy (Lieffers and Stadt 1994) it is clear that C. canadensis has sufficient available light to ensure survival in the understory of many mixed-wood stands.

The observation of higher g_s in shade-plants, over all light levels, is opposite to what has been reported elsewhere (Björkman 1981; Farquhar and Sharkey 1982). The reasons for this are unclear. The higher observed stomatal conductance rates in shade plants were not associated with higher rates of net assimilation, and would therefore lead to a reduction in water use efficiency. High rates of water loss in shade plants may not be detrimental, however. In natural understory environments actual transpiration rates may be lower than in open conditions because of lower vapour pressure deficits and lower leaf temperatures (Oke 1987). Higher stomatal conductances may facilitate optimum internal leaf CO_2 concentrations with little added cost in terms of water loss. The plants in this study were maintained in a well-watered condition and the shade frames would have reduced vapour pressure deficits. It is unlikely if these plants had experienced any significant water stress during this experiment. Whether native populations of understory plants would also react this way is not known.

Faster rates of stomatal opening relative to closing were found in C. canadensis and have been reported in a number of other graminoid species (Fay and Knapp 1993; Knapp 1993). The presence of a time lag in the stomatal opening response has only been reported in cultivated oats (Avena sativa L.) (Fay and Knapp 1993). The time lag in g_s response to high light negated the faster opening rate, so that the overall opening and closing response times did not differ. NA, however, showed an immediate increase after the resumption of high light despite the lag in the stomatal response. Nonetheless, the time lag in g_s likely reduced the speed of recovery in NA because internal CO_2 concentrations would be sub-optimal. Immediately after the re-introduction of high light, a reduction in internal CO_2, concurrent with an increase in NA, was observed which suggests a stomatal limitation to NA, at least over the short term (Farquhar and Sharkey 1982). The slow stomatal closure response yet rapid opening would act to maintain a high internal CO_2 level in conditions of continuous high light interspersed with short periods of low light. This should maximise carbon assimilation through a faster NA recovery upon return to high light (barring biochemical limitations of NA). In the opposite conditions of extended low light with infrequent high light events these stomatal responses would tend to maintain closed stomata, thereby reducing the effective use of these short periods of high fluence light.

C. canadensis is found on a wide range of moisture and nutrient habitats, and spans the light regime from light forest shade to open meadows where it can form continuous dense sods (Watson et al. 1980). Stand composition in the mixed-wood boreal forests of western Canada ranges from pure aspen (*Populus tremuloides* Michx.) to mixtures of aspen and white spruce (*Picea glauca* (Michx) Voss) and to nearly pure white spruce. Where it is found in the forest understory, *C. canadensis* is most abundant and productive under the thin canopies of aspen. The relatively high ambient light levels in the older stands, where summer light levels average 30% of open conditions (Lieffers and Stadt 1994; Constabel 1995), will enable considerable growth. The flat petioles of aspen leaves cause them to flutter in the wind, resulting in a light regime in the lower canopy dominated by very frequent, short duration, high fluence sunflecks (Roden and Pearcy 1993). Rapid successive sunflecks can bring about photosynthetic induction in some understory plants (Chazdon and Pearcy 1986) and may act in a similar way in *C. canadensis* under a canopy of aspen. *C. canadensis* abundance is severely reduced when the canopy is composed of a large percentage of white spruce (Powelson and Lieffers 1991; Lieffers and Stadt 1994). The dense white spruce crowns produce extended periods of shade which would induce stomatal closure and would be the most limiting to carbon assimilation given the nature of this grass's response to variable light.

Low light compensation points, especially in shade plants (near 15 μmol m^{-2} s^{-1}), should ensure that *C. canadensis* can survive in the understory of the mixed-wood boreal forest but not in the heavier shade of conifer dominated stands. However, the nature of the stomatal response to variable light suggests a photosynthetic system not efficient at utilising sunflecks or brief periods of high light interspersed with extended periods of low light. Rather its photosystem appears adapted to the more or less continuous light conditions typical of open environments, or the relatively high light conditions of older aspen stands. High assimilation rates in shade-grown plants will enable them to fully utilise periods of high light provided they are of sufficient length.

Thus despite the fact that, over succession, *C. canadensis* is restricted to the understory of forest stands, its photosynthetic adaptations appear to make it suited to meadow conditions. Since the boreal forest is a relatively young community (Ritchie 1987) species capable of utilising a wide range of light conditions such as *C. canadensis*, may be able to dominate a wide range of habitats. It may be the lack of effective competitors in the understory, particularly those of greater height (Chapter 5) that permits *C. canadensis* to occupy such sites despite a photosynthetic system apparently suited for open environments.

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Table 4-1. C. canadensis mean (± 1 SE) stomatal conductance to water vapour over time with changes in photosynthetic photon flux density. Data derived from sigmoidal curves fit to data from each of four plants and linear regression through linear portion of response curve for each plant.

Variable	Opening[1]	Closing[2]	P value[3]
Time to Achieve 20% of Maximum Response (min)	2.44 ± 0.22	1.25 ± 0.01	0.015
Slope at Inflection Point (mmol m^{-2} s^{-1} / min)	34.79 ± 6.47	-19.02 ± 1.54	0.006
Slope of linear response curve (mmol m^{-2} s^{-1} /min)	23.[illegible] ± 2.96	-16.83 ± 2.41	0.008
Time to Achieve 80% of Maximum Response (min)	4.49 ± 0.50	4.38 ± 0.41	0.708

[1] Opening refers to changes following transition from low to high light.

[2] Closing refers to changes following transition from high to low light.

[3] Probability for paired T-test of differences in absolute opening and closing values.

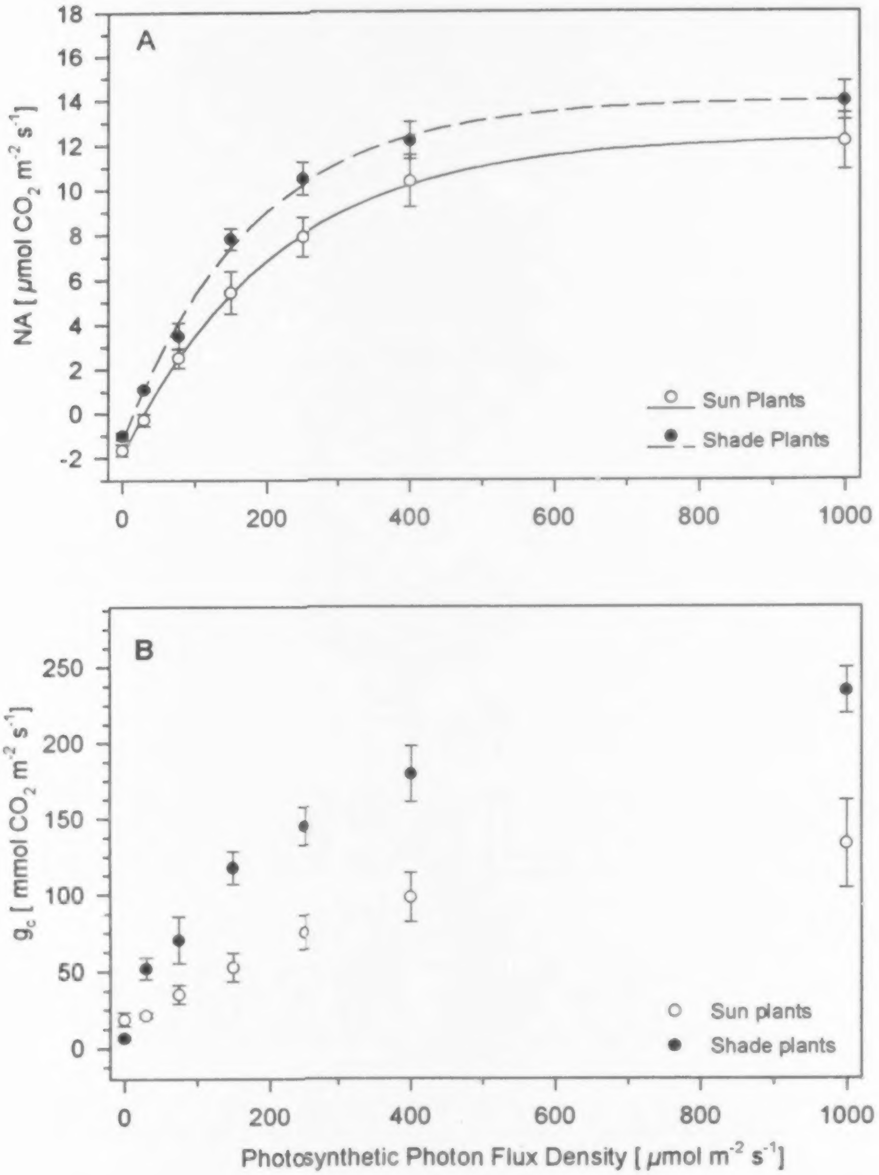

Figure 4-1. Photosynthetic light response curves in C. canadensis for shade and sun grown plants. Net assimilation (a) and stomatal conductance to carbon dioxide (b) means ±1 SE are shown together with best fit non-linear regression lines. Five plants per light condition were measured.

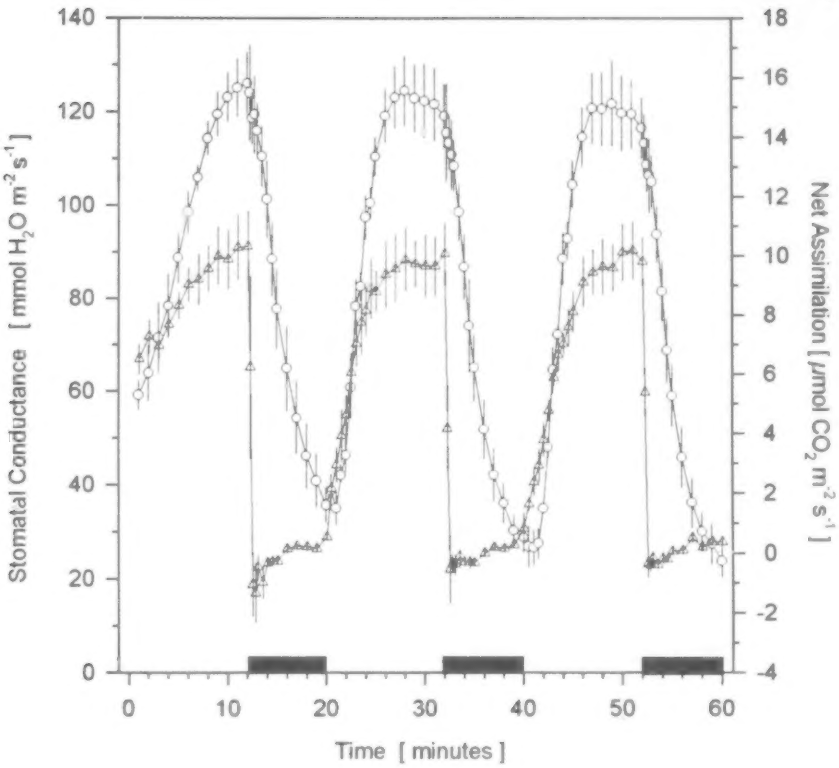

Figure 4-2. Net assimilation (triangles) and stomatal conductance to water vapour (circles) in C. canadensis in response to alternating high (615 µmol m^{-2} s^{-1}) and low (33 µmol m^{-2} s^{-1}) light. Dark bars on x-axis indicate 8 min periods of low light. Means ±1 SE of four plants are shown.

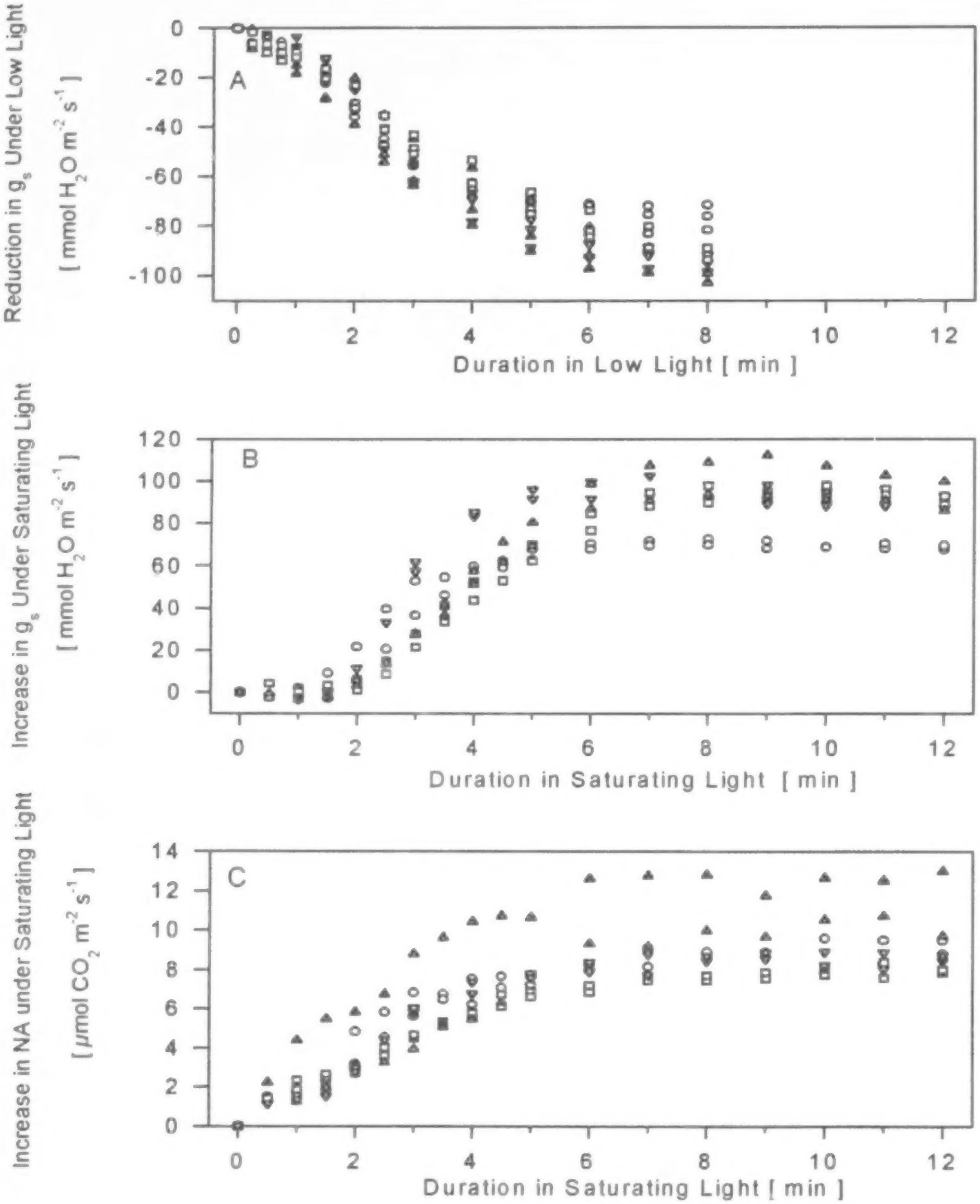

Figure 4-3. Decrease (a) and increase (b) in stomatal conductance (g_s) with time since abrupt change in light level. Increase in net assimilation (NA) with time since resumption of high light (c). Symbols indicate individual plants responses from two increasing and three decreasing phases for each of the four plants.

Chapter Five

Photosynthetic light response of four boreal forest understory shrubs

Introduction

A major limiting factor for growth of all forest understory species is the availability of light. Persistence in the understory necessitates a photosynthetic system adapted to low light and characterised by low photosynthetic light compensation points, low respiration rates and relatively low light saturated photosynthetic rates (Björkman 1981). Landscapes subject to recurrent disturbances provide spatially and temporally changing light environments. Shaded understories are transformed to open areas after disturbance and species capable of exploiting both environments should thrive.

Corylus cornuta Marsh.(beaked hazel, filbert), Lonicera involucrata (Richards.) Banks (honeysuckle, black twinberry), Rosa acicularis Lindl. (prickly rose) and Rubus idaeus L. (wild red raspberry) are widespread in the boreal forest and are economically important competitors to young white spruce (Haeussler et al. 1990; Bell 1991). These species represent three different taxonomic families and a range of growth habits. Rose is common in the understory of deciduous and some coniferous stands where it is typically found as a single stem less than 1 m. It will dominate the shrub layer in open areas, however (Viereck and Little 1972; Watson et al. 1980; Haeussler, et al. 1990). Honeysuckle is also less than 1 m. tall with few stems. It tolerates the shade of broad leafed forests but produces the most vigorous growth in full light (Klinka et al. 1989; Haeussler et al. 1990). Considered as moderately shade tolerant (Klinka et al. 1989; Haeussler et al. 1990), raspberry plants made up of several stems can be up to 1.5 m in height in the understory and can form dense thickets in recently disturbed areas (Core 1974; Klinka et al. 1989). Hazel may form thickets of up to 2 m in height in both the understory of open deciduous and mixed-wood stands in British Colombia (Haeussler et al. 1990) and jack pine (Pinus banksiana Marsh.) and red pine (P. resinosa Ait) stands in northern Minnesota (Tappeiner 1971; Tappeiner and John 1973). Near 30% of full sunlight in necessary for best growth of hazel and dense thickets may form when it grows in the open (Sterns 1974). Although the basic descriptive and reproductive biology of these shrubs has been reviewed (Gill and Healy 1974; Watson et al. 1980; Haeussler et al. 1990), no published works describe the ecophysiology of these species.

The boreal forest is dominated by large scale fires which create a mosaic of stands of various ages (Payette 1992). Many boreal forest shrub species may form dense thickets and dominate a site in the period immediately after disturbance (Viereck and Little 1972; Watson et al. 1980; Haeussler et al. 1990; Bell 1991). The eventual recruitment of trees onto the site will force the shrubs into the understory. To ensure their survival they must be able to photosynthesise in the low fluence light of the understory. This would necessitate a photosynthetic system adapted to low light and characterised by low respiration rates as well as low light compensation points (Björkman 1981). lkjh This study reports on the nature of the photosynthetic system of four shrub species in natural understory conditions of the mixed-wood boreal forest. It is the first report of these species' photosynthetic response to light measured under field conditions.

Materials and Methods

Two aspen dominated forested areas were selected for this study. White Mud Park is an urban natural forested park covering several kilometres of the North Saskatchewan River valley within the City of Edmonton, Alberta (113° 30' W, 53° 30' N). Stands in White Mud Park selected for this study consisted of 20-30 year old aspen with a thin canopy and a vigorous understory shrub layer. The second site, Isle Lake, (115° 35' W, 53° 45' N) located 80 km west of Edmonton, Alberta, was dominated by aspen stands of similar age and canopy closure to that of the White Mud Park site. The four selected species (*C. cornuta*, *L. involucrata*, *Rosa acicularis* and *Rubus idaeus*) were common understory shrubs at both sites: At each site a total of ten plants of each species was measured. On any one day, two blocks (approximately 5 m by 5 m) containing all four species were measured. Measurements at White Mud Park were made between July 7-16 and at Isle Lake between July 20-29, 1993. Within each site, ten areas were selected where all four study species co-occurred. Thus within each site, an area of approximately 5 ha was sampled during the course of the experiment.

Only apparently healthy and undamaged plants were used. Photosynthesis was measured between 09:00 and 17:00 hrs on fully mature leaves. In hazel and honeysuckle the third leaf from the branch apex was selected, while in rose and raspberry the terminal leaflet of the third leaf was used. Following photosynthesis measurement the leaves were transported to the laboratory and the total chlorophyll was extracted in dimethyl sulfoxide. Optical densities were measured at 645 nm and 665 nm (Ronen and Galun 1984), and the chlorophyll concentration was calculated using the equations of Arnon (1949). It was expressed on a projected leaf area basis (mg cm^{-2}).

Photosynthetic response to light was measured with a portable infrared gas analyser (IRGA) (ADC LCA2 or LCA3, Analytical Development Company, Hoddesdon, England) using a conifer cuvette (PLC(C)). Variable photosynthetic photon flux densities (PPFD) were produced with a custom built controller. Light was supplied by a 75W, 12V quartz halogen lamp powered from a 18 V power supply regulated to a steady 12 V. This ensured that no spectral changes in light occurred as the cells discharged. The light was passed through a 50mm camera lens and a precision digital servo motor regulated the camera diaphragm to give fine control over light quantity. Even light coverage over the entire leaf chamber was ensured with a pair of custom ground lens elements mounted between the camera lens and the leaf chamber. At very small apertures, however, the lens could not adequately spread the incoming light. To produce low PPFD, therefore, neutral density filters were used in conjunction with the camera lens diaphragm.

Based on initial trials with each species, four light levels were selected. In addition one dark respiration measurement was made on each plant. The PPFDs were selected to ensure that three measurements were made over the linear portion of the light response curve and two on the saturation phase. PPFD was measured inside the leaf chamber at the position of the leaf surface with a quantum sensor (Li-Cor 190s, Lambda Instruments, Lincoln, Nebraska). For hazel the PPFDs used were 0, 59, 207, 737, 1081 μmol m^{-2} s^{-1} ; for rose they were 0, 36, 133, 737, 1081 μmol m^{-2} s^{-1} ; and for both honeysuckle and raspberry the PPFDs used were 0, 59, 150, 540, 1081 μmol m^{-2} s^{-1}. The entire light assembly and cuvette were enclosed in a heavy cloth bag to exclude ambient light. In-going relative humidity was maintained near 30% and leaf temperature was measured with a fine wire copper-constantan thermocouple appressed to the underside of the leaf.

Leaf area was determined using a leaf area meter (Li-Cor 3100, Lambda Instruments Corporation, Lincoln, Nebraska). All photosynthesis measurements were expressed on a projected leaf area basis. Net assimilation (NA, μmol CO_2 m^{-2} s^{-1}), transpiration (E, mmol H_2O m^{-2} s^{-1}) and water use efficiency (WUE, mmol H_2O transpired / μmol CO_2 fixed) were calculated according to the equations of von Caemmerer and Farquhar (1981). Residual conductance of CO_2 (g_r, mmol m^{-2} s^{-1}) was calculated as NA / internal CO_2 concentration (Jones, 1985). For each plant the net photosynthetic response to PPFD data were fit by least squares iterative non-linear regression techniques to the monomolecular function (Causton and Dale, 1990). Derived measures from each plant's modelled curves were: photosynthetic light compensation point (μmol photon m^{-2} s^{-1}), dark respiration rate (R, μmol CO_2 m^{-2} s^{-1}) and light saturated net photosynthetic rate

(A_{max}, µmol CO_2 m^{-2} s^{-1}) (Causton and Dale 1990). An estimate of the quantum yield (µmol CO_2 $µmol^{-1}$ photon) based on incident light was also made, however it is termed photochemical efficiency in this study to differentiate it from true quantum yield. The modelled light response curves required that data below the light compensation point be used and the inclusion of these data will over-estimate true quantum yield (Sharp et al. 1984).

To assess overall differences between species' photosynthetic responses to light, the net assimilation rates of all plants of a species, at each site, were regressed against incident PPFD. The response curves were tested for coincidence of regression lines t (Potvin et al. 1990). Analysis of variance (ANOVA) was used to test for differences among species in: gas exchange variables at maximum supplied PPFD, variables derived from the modelled light response curves, and chlorophyll concentrations. The ANOVA model was a nested mixed model with DAY nested within SITE and two replicates within DAY. SITE and DAY were random, however the pure error term was used to test the main effect SPECIES since the variation between species was best estimated by this term rather than the interaction of SITE and SPECIES. Pure error was also used to test the interaction effect of SPECIES by DAY. The SPECIES by DAY interaction term used to test the SITE by SPECIES interaction. SITE effects were tested with the DAY within SITE error term. Differences between species' mean gas exchange responses were compared with Scheffé's procedure.

Results

Measured Gas Exchange Variables

Hazel, raspberry and honeysuckle had similar, and relatively low measured net assimilation rates at saturating PPFD ranging from 4 to 6 µmol CO_2 m^{-2} s^{-1}, while rose photosynthesised at a rate of 7-8 µmol CO_2 m^{-2} s^{-1} (Fig. 5-1, Table 5-1). At both sites, the photosynthetic response of rose to PPFD (Fig. 5-1) was significantly different from that of the other three species (Isle Lake, $F_{4,192} = 34.6$, $P < 0.0001$; White Mud Park, $F_{4,192} = 47.6$, $P < 0.0001$). At White Mud Park, no significant differences among raspberry, hazel and honeysuckle light response curves were evident, however, at Isle Lake, the honeysuckle light response curve differed from that of hazel and raspberry ($F_{4,142} = 4.88$, $P = 0.001$) (Fig. 5-1).

Significant effects of SITE were found for transpiration (E), net assimilation (NA), and residual conductance (g_r) ($P < 0.05$). White Mud Park generally had higher mean values for these variables (Table 5-1). Since these sites were randomly selected no inherent site differences were obvious. Weather conditions, characterised by an above-average number of rainy days prior to and during the entire study, were similar at both sites. No significant SITE by SPECIES interactions were found in any of the measured gas exchange variables.

At maximum PPFD (1081 μmol m^{-2} s^{-1}), average E, NA, and g_r differed significantly among species ($P < 0.001$); while no differences in mean g_c or WUE were found (Table 5-1). At both sites, mean NA, g_r and E in rose were significantly higher than the other three species ($P < 0.05$). Although the overall photosynthetic response to PPFD of honeysuckle at Isle Lake was different from that of raspberry and hazel, individual gas exchange variables were not different among these three species (Table 5-1).

Light Response Curve Derived Variables

Mean photosynthetic light compensation points did not differ between sites or amoung species (Fig. 5-2A). Significant SITE by SPECIES interactions ($P < 0.001$) were found for both photochemical efficiency and respiration rate, due largely to the high values for these variables in rose at the White Mud Park site only (Fig. 5-2B,C). The mean rose response was contrasted to the mean response of the remaining three species within each site, and the Dunn-Šidák method used to adjust α because of the non-orthogonality of these contrasts (Sokal and Rohlf, 1981). Based on these contrasts, the rose photochemical efficiencies were higher ($P < 0.001$) than hazel, honeysuckle or raspberry at White Mud Park but not at Isle Lake ($P = 0.24$). Higher dark respiration rates (R) in rose were offset by a greater apparent photochemical efficiency so that light compensation points were similar among the four species and between sites ($P = 0.73$, and $P = 0.68$ respectively). Light compensation points were typically less than 50 μmol m^{-2} s^{-1} in all species (Fig. 5-2A). Rose clearly had a greater photochemical efficiency at White Mud Park relative to Isle Lake (Fig. 5-2B). Therefore, the difference in photochemical efficiency between sites was contrasted based on the hazel, honeysuckle and raspberry data only, and showed a higher photochemical efficiency in White Mud Park relative to Isle Lake ($P < 0.001$) (Fig. 5-2B). The pattern in R mirrored that of the photochemical efficiency, with higher rates at White Mud Park versus Isle Lake, ($P < 0.001$) and rose at White Mud Park again had higher R than hazel, honeysuckle, or raspberry ($P < 0.001$) (Fig. 5-2C). No differences in R were found among hazel, honeysuckle or raspberry at Isle Lake ($P = 0.29$). Significantly different A_{max} was found among the species across both sites ($P < 0.001$) (Fig. 5-2c). Rose had considerably higher A_{max} than honeysuckle, hazel or raspberry (8.2 vs 5.6, 4.7, 4.6 μmol CO_2 m^{-2} s^{-1}, respectively, $P < 0.05$).

Chlorophyll concentrations (leaf area basis) differed by species and site (Table 5-1). A significant chlorophyll SITE by SPECIES interaction effect was found. No interaction or site effect was found for hazel, honeysuckle and rose when analysed without the raspberry data. Among these three species, rose had higher chlorophyll concentrations than hazel or honeysuckle ($P < 0.05$).

Discussion

Despite the range in growth habits and differences in taxonomic groupings among rose, hazel, honeysuckle, and raspberry, their photosynthetic response to light was similar, with only rose differing significantly. A higher NA over all light intensities, and a significantly higher A_{max}, would enable rose to have a greater carbon assimilation potential at any light level compared to the other shrub species. Chlorophyll concentrations were higher in rose and may account for greater assimilation rates through increased light absorption (Björkman 1981). Higher residual conductance, and greater photochemical efficiencies and respiration rates in the White Mud site suggest that non-stomatal processes of photosynthesis facilitated the greater carbon assimilation capacity observed in rose. Higher photosynthetic efficiencies are generally associated with higher respiration rates needed to maintain greater levels of photosynthetic constituents (Björkman 1981).

All species studied had low light compensation points ranging from 35 - 40 $\mu mol\ m^{-2}\ s^{-1}$. These levels are lower than typical ambient understory light found in most deciduous dominated mixed-woods (Lieffers and Stadt 1994; Constabel 1995). Instantaneous light compensation points, however, are not indicative of the true light level necessary for photosynthesis to balance respiratory carbon demands on a whole plant basis. The additional costs of leaf, stem, and root construction, and their night-time respiration place the "ecological" light compensation point considerably higher than the instantaneous light compensation points as measured here (Givnish 1988). The cost of perennial aerial structures increases with plant height as may the proportion of total plant biomass made up of non-photosynthetic supporting tissue (Raven 1986). The large stature of these shrubs, in particular hazel, would increase the whole plant light compensation point and effectively reduce carbon supply for additional growth at low PPFD. However, the photosynthetic systems of these species would likely enable a modest carbon gain in most mixed-wood understories.

Modest growth is also likely given the low light saturated photosynthetic rates in these shrubs. The maximum measured light saturated net assimilation rate was in rose, at 8 μmol m^{-2} s^{-1}. This is half the rate found in Calamagrostis canadensis (Michx) Beauv., a common grass found in similar understory conditions (Chapter 4), and less than a third the rate reported for aspen (Roden and Pearcy 1993). The reduced flowering and seed production in shaded conditions, reported for rose (Smithberg and Gill 1974) and hazel (Hsuing 1951 cited in Sterns 1974) is further evidence of limited carbon availability. A re-allocation of carbon in shaded environments away from flowering and into light harvesting apparatus is a common strategy in many plants (Grime 1981; Bazzaz et al. 1987).

These shrub species appear to have some adaptation to understory light conditions. Reduced respiration rates and low light compensation points as was found in these shrubs is expected in plants growing in low light (Boardman 1977; Björkman1981). However, it appears that limited carbon availability from low photosynthetic rates even at saturating light would prevent these species from flourishing in the understory.

The photosynthetic adaptations in these shrubs appear less related to maximising productivity in an understory environment than to ensuring a persistence there. It is likely that characteristics favouring growth and expansion may be of secondary importance to simply surviving in the understory. Disturbances, such as recurrent fires, periodically convert forested environments to open areas. However, post-fire site domination depends largely on the rapidity of propagule dissemination and establishment. Those individuals able to establish first, are likely to dominate the site until they are out-competed by species of a larger stature. A common fire-adapted method of plant propagation is vegetative reproduction (Payette 1992). Despite the loss of above-ground biomass after a fire, immediate site re-colonisation is made possible by under-ground regenerating organs. The four species in this study can reproduce vegetatively from below-ground rhizomes, root buds or basal sprouts (Haeussler et al. 1990). Low photosynthetic rates in the understory, are sufficient to maintain the below-ground regenerating structures and hence permit the existence during the interval between fire events. This in turn will increase the chances of rapid post-disturbance site re-colonisation and permit rapid growth and expansion that has been commonly reported for these species under open conditions.

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Table 5-1. Gas exchange variables and leaf chlorophyll concentrations in understory shrubs at Isle Lake (ISL) and White Mud Park (WMP) sites. Photosynthesis variables measured at PPFD=1081 μmol m^{-2} s^{-1}. Transpiration (E), net assimilation (NA), residual conductance (g_r), and water use efficiency (WUE) means ± 1 SE of 10 plants per species are shown.

Site	Species	E (mmol m^{-2} s^{-1})	NA (μmol m^{-2} s^{-1})	g_r (mmol m^{-2} s^{-1})	WUE (μmol photon / mmol H_2O	Chlorophyll (mg cm^{-2})
ISL	Corylus	1.5 ± 0.1	4.0 ± 0.3	11.6 ± 0.8	2.7 ± 0.2	0.029 ± 0.0017
ISL	Lonicera	1.4 ± 0.1	4.9 ± 0.4	14.0 ± 1.2	2.9 ± 0.2	0.027 ± 0.0014
ISL	Rosa	2.4 ± 0.3	7.2 ± 0.7	21.0 ± 2.1	2.9 ± 0.2	0.034 ± 0.0016
ISL	Rubus	2.2 ± 0.3	3.7 ± 0.4	10.7 ± 1.2	2.5 ± 0.2	0.024 ± 0.0015
WMP	Corylus	1.9 ± 0.1	5.4 ± 0.3	15.7 ± 0.7	2.9 ± 0.2	0.027 ± 0.0013
WMP	Lonicera	1.9 ± 0.1	6.2 ± 0.6	17.7 ± 1.7	3.2 ± 0.3	0.029 ± 0.0024
WMP	Rosa	3.5 ± 0.5	8.8 ± 0.7	25.7 ± 2.2	2.7 ± 0.2	0.031 ± 0.0013
WMP	Rubus	2.1 ± 0.2	5.9 ± 0.5	17.2 ± 1.4	2.9 ± 0.2	0.028 ± 0.0011

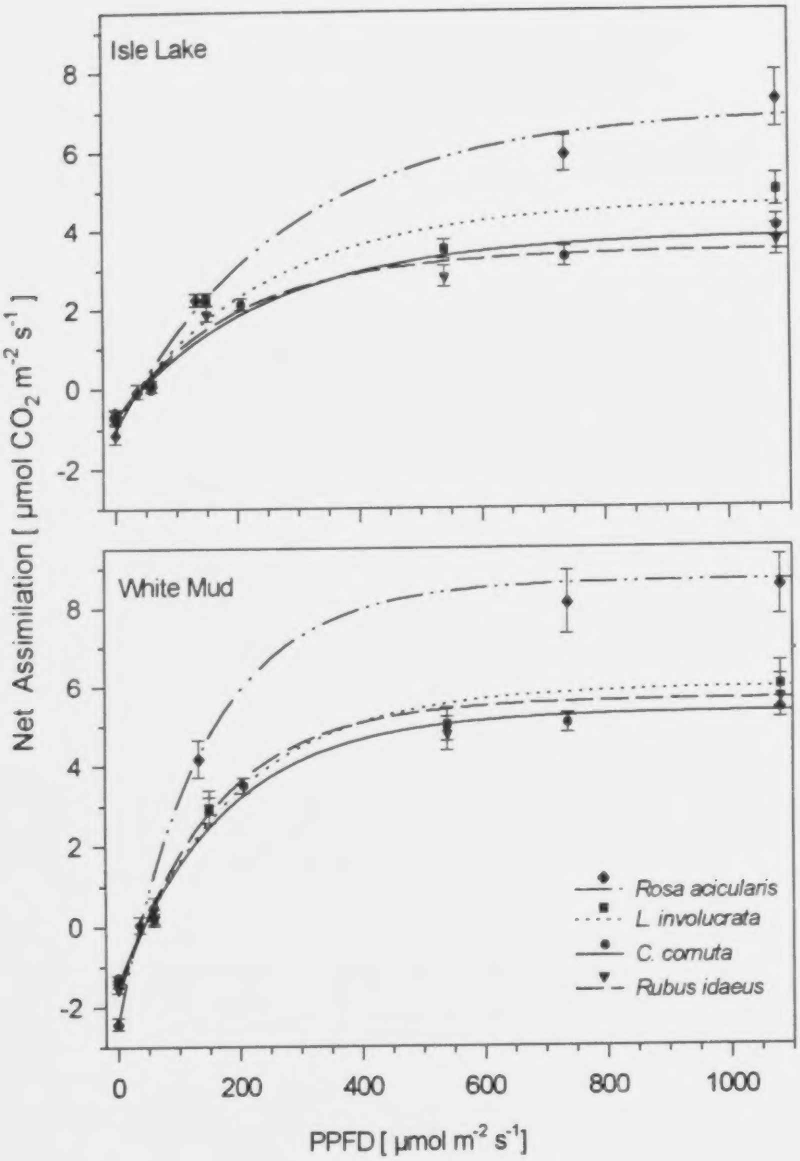

Figure 5-1. Modelled light response curves of Rosa acicularis, Lonicera involucrata, Corylus cornuta, and Rubus idaeus growing in a boreal mixed-wood understory on two sites. Non-linear regression lines were fit to data from 10 plants per species per site. Symbols are mean (±1 SE) species net assimilation rates at each photosynthetic photon flux density (PPFD).

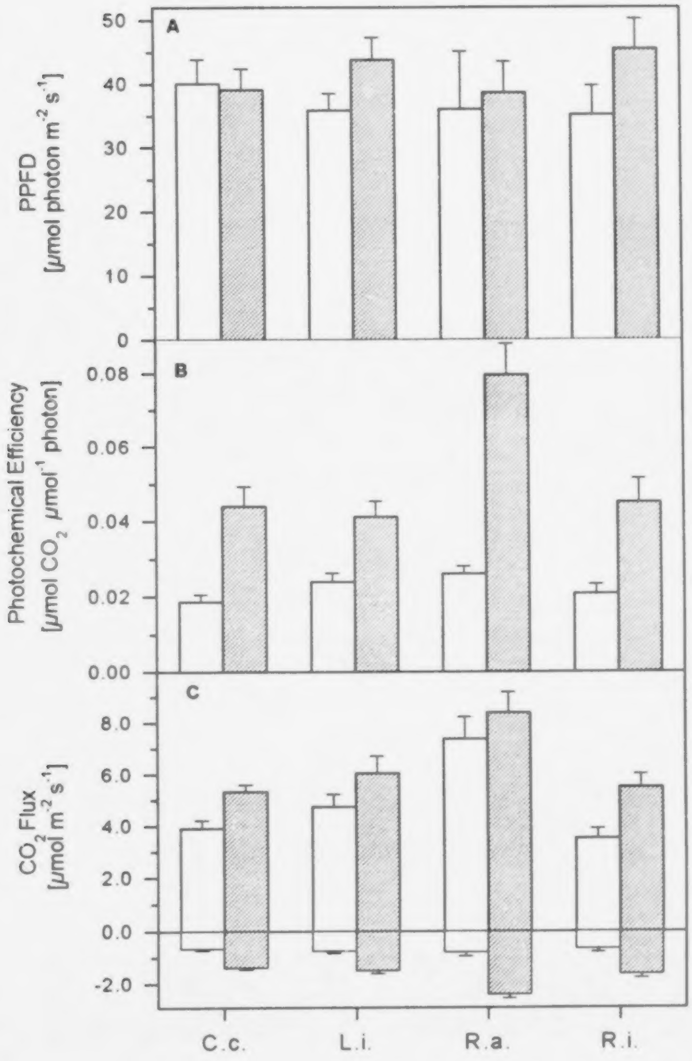

Figure 5-2. Derived variables of (A) light compensation point, (B) photochemical efficiency and (C) light saturated net assimilation and dark respiration rates in: Corylus cornuta (C.c.), Lonicera involucrata (L.i.), Rosa acicularis (R.a.), and Rubus idaeus (R.i.) growing in the understory at White Mud Park (hatched bars) and Isle Lake (open bars) sites. Variables were derived from modelled non-linear regression lines fit to individual plants. Means ±1 SE (vertical bars) of 10 plants per site per species are shown.

Chapter Six
Synthesis

Temporal variability in the light environment may have immediate as well as long term effects on plant fitness and distribution of species. This series of studies has shown that photosynthetic acclimation to high fluence light in understory spruce released from an overstory, can provide an immediate increase in carbon assimilation potential. Changes to crown and shoot morphology and continued photosynthetic acclimation will provide additional benefits to plant carbon gain within two to three years. This considerable acclimation potential of the photosystem and shoot morphology has enabled this species to successfully compete in a variety of light environments.

Lodgepole pine, in contrast, has an apparently non-plastic photosynthetic system adapted to full sunlight. The high temperature necessary to open its serotinous cones limits its potential regeneration sites to open areas (typically after fire). Maximum utilisation of an open site's resources, including a photosystem adapted to full sunlight, will facilitate the rapid growth rate characteristic of this pioneer species. The photosystems of these two trees are adapted to maximise the use of light levels characteristic of the conditions in which they are likely to regenerate and grow. Over the life-time of pine, these light conditions are likely to be relatively constant, whereas, in spruce, they are likely to be highly variable.

The ability to maintain a positive carbon balance in the low fluence light of an understory is essential for survival, and understory rose, hazel, honeysuckle, raspberry, and C. canadensis have the ability to do so under canopies of aspen or aspen-dominated mixed-woods. The low photosynthetic rates at saturating light, and the energy necessary for the maintenance of woody supporting tissue in the shrubs, will likely restrict the energy available for growth and expansion in understory individuals. Thus, it would appear, that these shrubs have limited adaptations to understory light levels. Although the nature of these shrubs' photosynthetic rates in full sunlight is unknown; the reports of rapid expansion and dense thicket formation soon after disturbance (Haeussler et al. 1990) suggest that they are capable of fully utilising full sunlight. The photosystem of C. canadensis is characterised by low light compensation points, and light-saturated photosynthetic rates considerably higher than the shrubs. Its herbaceous nature will reduce the amount of energy necessary for plant maintenance and this, coupled with its photosynthetic capabilities, will enable it to grow under a wide range of overstory canopies. As with the shrubs, however, rapid growth and expansion occur predominantly in open sites (Laughlin et al. 1984). The shrubs and C. canadensis flourish in open conditions (with photosystems apparently adapted to such conditions) yet can also maintain a presence in the understory of many mixed-wood stands. Given the limited adaptations of these species' photosystems to understory light conditions, there would appear to be no immediate advantage to persisting in forested environments.

The dominant successional force in the boreal forest is fire (Heinselman 1981, Payette 1992). Recurrent disturbances re-start the process of succession by converting treed areas in to open sites. For species subjected to such recurrent disturbances, survival may be more a function of their ability (or inability) to regenerate after disturbance, than of their photosynthetic abilities under varying light regimes. The regularity of fire in the boreal forest has lead to various fire-adapted regeneration mechanism in many of the species found in it (Heinselman 1981). Lodgepole pine's serotinous cones, and the underground rhizomes of the shrubs and C. canadensis enable them to remain on-site after most fires. The fire-dependent regeneration mechanisms in pine dictate a light environment dominated by full sunlight during seedling establishment and the rapid growth rates should ensure the tree crowns remain above much of the competing vegetation. Similarly, below ground vegetative reproduction systems in the shrubs and C. canadensis will enable them to quickly re-establish in the open, full sunlight of recently burned sites. Photosynthetic adaptations to full light in these species should enable rapid growth and ensure site re-vegetation soon after disturbance. The limited shade adaptations in the shrubs and C. canadensis are sufficient to ensure that a presence in the understory is maintained, however, they will not allow for appreciable growth.

In contrast to the other species studied, white spruce does not reproduce vegetatively, does not have serotinous cones and has irregular seed crops (Neinstaedt and Zasada 1990), and so lacks the adaptations necessary to remain on-site after a fire. It must therefore, compete with all other vegetation in order to become established on a recently disturbed area. It is likely to be confined initially to the understory of a shrub or grass layer and later, possibly a hardwood canopy. It will, therefore, naturally be subjected to considerable light variability over its life span. Photosynthetic adaptations to low fluence light will enable it to grow in the understory. White spruce individuals released from an overstory canopy can rapidly acclimate their photosystems and within several years alter shoot and crown morphology to optimise the use of the higher light levels. Unlike the true firs, it does not appear to reduce height growth in favour of lateral branch growth when in the low light of the understory. The maintenance of height growth in the understory may enable it to effectively compete for the available light if it is able to keep much of its crown above other understory vegetation.

It is apparent then, that adaptations to light variability must be assessed in the context of plant life-history. Thus, while P. contorta, C. cornuta, L. involucrata, R. acicularis, R. idaeus, and C. canadensis may not possess photosystems adapted to the low fluence light typical of the understory, they are capable, if necessary, of exploiting these environments to ensure the species survival in the landscape. Lodgepole pine can maintain a canopy position and remain unshaded, the others are able to survive in the shade of mixed-wood stands.

P. glauca lacks the disturbance-adapted regeneration mechanisms shared by the former species, however it can grow in highly variable light environments to which it is commonly subjected.

Silvicultural Implications

Retention of understory spruce advanced regeneration after the canopy aspen are harvested is presently being practised on mixed-wood sites in Alberta and elsewhere (Brace and Bella 1988). After several years lag time, increased diameter growth has been found in released advanced regeneration (Yang 1989; Navratil et al. 1994). The evidence from this work indicates that rapid physiological acclimation and longer term morphological and continued physiological changes can significantly increase sapling stage white spruce carbon assimilation potential. The timing of release of understory sapling spruce appears not to have substantial effects on its acclimation abilities. However, the large effect of climatic conditions, and the unknown effect of population differences, in mediating the response to release, limits the transferability of these findings. Greater replication over multiple years and geographic regions are necessary to corroborate these findings. This is particularly true with respect to growth responses to release.

The understory shrubs studied here and C. canadensis survive in the understories of many mixed-wood stands. Partial-cutting systems that remove portions of the canopy will increase light levels in the understory, and will likely enhance the growth of understory plants. If white spruce seedling recruitment is needed to supplement the existing advanced regeneration, a greater shrub density will impede seedling establishment and growth. C. canadensis will react in a similar fashion and particularly on sites with sparse white spruce advanced regeneration, understory plants may pose problems for the natural regeneration of white spruce.

The characteristics of the photosynthetic response to light in the shrubs, grass and spruce are similar enough that management of understory competitors to white spruce, through manipulation of the light levels reaching the forest floor, will be difficult. The ability of the to maintain positive photosynthesis under very low light levels provides a very narrow window of light levels that would be preferentially used by the spruce. However, in mixed-wood stands with a dense white spruce understory of advanced regeneration, partial-cut systems may be applied to yield a limited increase in understory light. While this may temporarily increase all understory plant growth, the development of the spruce canopy will subsequently greatly reduce understory light levels and hence, understory plant growth.

Further Research

Several areas of research pertaining to the issues raised in these studies still require more work. A better quantification of the nature of the variability in light beneath mixed-wood canopies, particularly in reference to the amount and distribution of periods of high fluence light, is needed. Recent studies (Lieffers and Stadt 1994; Constabel 1995) have provided valuable knowledge about the amount and seasonal distribution of understory light, and Roden and Pearcy (1993) have shown the importance of sunflecks in providing much of the lower canopy light in aspen stands. As has been shown in other forested systems, sunflecks that reach the forest floor may be critically important in understory species' ability to photosynthesis. This needs to be investigated in the mixed-wood boreal forest situation.

The ability of white spruce to acclimate to the very dramatic environmental changes after release is remarkable. Several aspects of this phenomenon have yet to be investigated. The possible role of the xanthophyll cycle in providing protection from excess radiant energy and the changes in pigments (chlorophylls) during the acclimation process needs to be examined. The role of changes in needle density and orientation in reducing the potential for photoinhibition, as well as the occurrence of photoinhibition also needs to be addressed in more detail. In addition to the morphological changes after release, there are very likely to be changes to needle anatomy, particularly in the packing of mesophyll cells. Studies to investigate these changes and the time frame over which they are made in response to release, would add to the knowledge of the nature of the acclimation process in white spruce.

A better understanding of the carbon budget in understory plants, in particular the woody shrubs, is required. The potential of understory plants to assimilate carbon as a result of differences in the timing of leaf-out in the overstory and understory species should be investigated. It is possible that annual carbon budgets may rely on periods of leaflessness in the overstory (fall and spring) in order to be balanced. Furthermore, the allocation of energy to photosynthetic versus non-photosynthetic biomass is needed to assess, particularly in the woody shrubs, what level of biomass is sustainable given the limitations to photosynthetic carbon gain from the low fluence understory light. It would also be of interest to assess the photosynthetic performance of these shrubs growing in the open in order to understand the extent to which 'sun' phenotypes may occur. Finally, some knowledge of the possibility and extent of within-clone resource translocation would be necessary to evaluate the potential for clones to utilise spatially variable resources. Intra-clone translocation of resources may allow ramets in patchy environments to acquire and share resources that are locally available.

The studies with C. canadensis and the stomatal tracking of net assimilation suggested poor ability to use sunflecks, however, more information is needed. The rapidity of the loss of photosynthetic induction under low light, and the relative contribution of biochemical and stomatal limitations to this induction will require detailed study. The apparent lack of sun and shade phenotypes in the species is intriguing, and deserves further study. The potential for sun and shade phenotype differences to be expressed only at extremely low fluence rates should be checked. The higher stomatal conductance rates in the shade plants relative to the sun plants suggests that perhaps the differences between sun and shade plant photosystems lays in their responses to variable light rather than constant light as investigated in this work. This possibility deserves further study.

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